BREEDING PROCEDURES AND SEED PRODUCTION MANAGEMENT IN PEARL MILLET X ELEPHANTGRASS HEXAPLOID HYBRIDS

By

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To Daniela, my true inspiration

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Chairperson: Dr. Stanley C. Schank
Major Department: Agronomy

Seeded pearl millet [*Pennisetum glaucum* (L.) R.Br.] x elephantgrass (*P. purpureum* Schum.) hexaploid hybrids possess many desirable attributes for forage and biomass production. A series of experiments was conducted over a period of four years to improve the efficiency of breeding programs, evaluate the success of different selection methodologies, and study possible management procedures for mechanizing seed harvest. The experiments were conducted at the Dairy Research Unit, University of Florida, during the years 1990 to 1993. Traits evaluated in the experiments included leaf length and width, tillers plant^{-1}, plant height, days to flowering, panicle length, panicles plant^{-1}, seeds panicle^{-1}, seed set, 100-seed weight, seed yield panicle^{-1}, and seed yield plant^{-1}. Single plant heritability estimates, correlations, and responses to selection were calculated from an experiment containing seven selfed (S_1) families. Path-coefficient analyses of seed yield components were also calculated to evaluate the effect of each component on total seed yield plant^{-1}. Recurrent restricted

phenotypic selection (RRPS) and mass selection (MS) were implemented on a population for two cycles of selection and then evaluated for progress. Selection emphasized higher seedling vigor, leafiness, tillers plant^{-1}, panicle length, intermediate height, and early flowering. In another experiment, three defoliation treatments (no cuts, two cuts, and three cuts per year) were imposed on four different genotypes to evaluate their effects on plant height, days to flowering, reproductive traits, and survival.

Single plant heritability estimates were very low to moderate (0.02 to 0.30) for the traits measured. Despite these low heritabilities, predicted responses to selection for reproductive traits were high due to large phenotypic variation. Path analyses of seed yield components indicated that selection for seeds panicle^{-1} and 100-seed weight would be most effective for improving seed yield plant^{-1}. Environmental influence was responsible for large differences between genetic and phenotypic correlations. Path analysis utilizing genetic correlations was more useful for developing selection criteria. RRPS was more effective than MS in improving the traits under selection. Realized heritabilities ranged mostly between 0.3-0.5 and were higher than the previously estimated heritability values. In the experiment evaluating possible management procedures for seed harvesting, the goal of achieving a reduction in the height and biomass of the plants, while maintaining adequate seed yield, was feasible with two cuts year^{-1} (mid June and beginning of August). Three cuts year^{-1} (last cut in mid-September) drastically reduced seed yield plant^{-1} and would not be recommended if seed were to be harvested. Guidelines for the improvement of pearl millet x elephantgrass hybrids as well as possible management practices for mechanized seed harvesting were established.

CHAPTER 1
INTRODUCTION

The interspecific hybrids between pearl millet [*Pennisetum glaucum* (L.) R.Br.] and elephantgrass (*Pennisetum purpureum* Schum.) are the most widely studied hybrids in the genus *Pennisetum* (Jauhar, 1981; Muldoon and Pearson, 1979). The purpose of obtaining this hybrid was to combine the high forage quality, seed production, nonshattering seed nature, and resistance to various diseases in pearl millet, with the aggressiveness, perenniality, and rust resistance of elephantgrass. The first person to document a man-made hybrid was Burton in 1941 (Burton, 1944). They were later produced in India (Krishnaswamy and Raman, 1949), Hawaii (Van Horn, 1947), South Africa (Gildenhuys, 1950), and Pakistan (Khan and Rahman, 1963), followed by other countries. In general, the hybrids are high yielding and more acceptable as forage plants than elephantgrass (Jauhar, 1981). Besides their use in livestock production (Schank and Diz, 1991), they possess great potential as a biomass energy crop (Schank, 1987) due to their high dry matter production. However, as with elephantgrass, they have to be vegetatively propagated. Pearl millet is an annual diploid, grown primarily for its grain and entirely seed propagated. Elephantgrass is a perennial tetraploid, which has low natural seed production and poor seed quality. Planting typically consists of placing whole stems horizontally in shallow furrows (Sollenberger et al., 1990; Woodard et al., 1985). High labor requirements and cost associated with establishment have limited the widespread use of this forage,

especially in developed countries. Pearl millet x elephantgrass hybrids are sterile triploids. During meiosis, chromatin bridges, formation of abnormal tetrads, and abortion of all four megaspores are usually observed (Hanna, 1981; Jauhar, 1981). Lack of availability of good quality seed in commercial quantities, use of poorly adapted genotypes, and lack of management expertise have limited commercial adoption of hybrids.

By doubling the chromosome number of the interspecific hybrid, fertility can be restored (Hanna, 1981). The amphiploids (hexaploids) obtained usually show a high degree of regular meiosis and their progenies have a wide range of pollen and seed fertility. Breeding at the hexaploid level is therefore possible. Amphiploids usually form 21 bivalents during meiosis (Jauhar and Singh, 1969), with multivalent associations rarely observed. This is due to the preferential pairing between the A-A, A'-A', and B-B genome chromosomes (Jauhar, 1981). This synthetic amphiploid would then behave meiotically like a typical allohexaploid. There is large heterosis for panicle size in the amphiploid. This greater panicle size, together with the high levels of male and female fertility due to regular meiosis, is the basis for obtaining a *Pennisetum* hybrid which can be seed propagated.

Further breeding of these grasses at the hexaploid level will be required if varieties are to be developed. In the hybrid *Pennisetum* breeding nurseries at the University of Florida, large phenotypic variability was measured in many important characteristics (Diz and Schank, 1993). Due to the existence of this variability, selection should be successful. Heritability estimates and genetic correlations would be very useful in improving the efficiency of a breeding program through the development of appropriate selection strategies. To date, heritability estimates and other genetic parameters for

these hybrids have not been published. They would be an important contribution to the future breeding of this interspecific hybrid.

Mass selection, based on the unreplicated phenotypic evaluation of individual plants, is one of the oldest crop-improvement techniques. Usually highly heritable traits have responded well to mass selection, but characteristics with low heritabilities and complex inheritance have not responded as well to this procedure (Sprague, 1955; Burton, 1974). Recurrent restricted phenotypic selection (RRPS) is a modified form of mass selection, where a number of restrictions are imposed to increase the efficiency of the method (Burton, 1974). Plants are selected from a grid arrangement in the field and selected phenotypes are intermated in isolation and close proximity in a greenhouse polycross, which ensures equal parental input as well as maximum recombination. Characteristics with low heritabilities should respond better to this modified form of mass selection. On the other hand, mass selection is simple, inexpensive, and rapid, and adequate progress is usually obtained with highly heritable traits.

A problem which remains to be solved prior to widespread use of the hybrids is mechanical seed harvesting. Plants which are not cut or grazed produce panicles at approximately 2.5 to 4.5 m in height, from the end of September to mid-November, at Gainesville, Florida (Diz and Schank, 1993). In order to mechanically harvest seeds, panicle height and plant biomass need to be reduced while seed production is maintained. This may be achieved through defoliation management, which would allow the dual use of the stand for forage and seed.

The objectives of this study can be divided into two main categories:

Seed production management: a) to evaluate the effects of three defoliation treatments on the height of panicles produced, date of flowering, seed yield components, seed yield plant^{-1}, seed germination, and plant survival in four *Pennisetum* hybrid genotypes; and b) to evaluate the correlations and compensatory effects among seed yield components under different defoliation treatments.

Breeding and selection: a) to determine the direct and indirect effects of seed yield components on seed yield through the use of path-coefficient analysis, and develop selection criteria for higher seed yield; b) to obtain heritability estimates and genetic, phenotypic, and environmental correlations for several vegetative and reproductive characters; c) to predict responses to selection and correlated responses for these characters; and d) to compare the progress obtained after two cycles of mass selection and recurrent restricted phenotypic selection (RRPS) in several important characters.

CHAPTER 2
LITERATURE REVIEW

Pearl Millet

Description, Origin, and Distribution

The genus *Pennisetum* is widely distributed throughout the tropics and subtropics of the world, comprising more than 140 different species. Pearl millet [*Pennisetum glaucum* (L.) R.Br.; synon. *P. typhoides* Stapf and Hubbard, *P. americanum* (L.) Leeke] is also commonly known as bulrush, cattail, or spiked millet. This species has developed numerous scientific names because of diverse treatment by different taxonomists (Jauhar, 1981). It belongs to the Gramineae family, the subfamily Panicoideae, the tribe Paniceae, the genus Pennisetum, and the section Penicillaria. Pearl millet is a robust, dual purpose annual grass which can range in height from 1.5-5 m (Krishnaswamy, 1962). Tillers arising from axillary buds produce a leafy growth with stems which are solid (Rachie and Majmudar, 1980). The leaves are long, usually 70-110 cm in length and 3-8 cm wide. The secondary root system is extremely profuse, sometimes penetrating 5 m under certain conditions (Rachie and Majmudar, 1980). This enables the species to grow in areas with very low rainfall, where harvests can be obtained with as little as 250 mm of annual rainfall (Jauhar, 1981). The inflorescence is a straight, cylindrical, solid, and unbranched panicle. Pearl millet is grown primarily for grain.

Krishnaswamy (1962) concluded that the center of origin of pearl millet was Africa, after a thorough evaluation of the *Pennisetum* species. Stapf and Hubbard (1934) already held this same view in 1934. Harlan (1971) suggested that the center of origin stretched from western Sudan to Senegal. The species was domesticated as a cereal in the southern margins of the Saharan central highlands approximately 4000-5000 years ago (Davies, 1968; Munson, 1975). Today it is widely distributed across the semi-arid tropics of Africa and Asia. It is the principal food crop across sub-Saharan Africa and north-western India (de Wet, 1987). It is also grown as a forage in southeastern U.S.A., Australia, South Africa and several other countries.

Seed Production and Propagation

The inflorescence of pearl millet is a terminal, dense, cylindrical panicle ranging in length from 10-150 cm and varying in color (Ferraris, 1973). On the average, there are about 1500 spikelets per panicle. The caryopses are globose to subcylindrical in shape, most often ash gray or steely blue in color, with a hard smooth cover. Color variants include purple, grayish brown, yellowish brown, and pearly amber-white. Seeds measure 3-4 mm in average, although seed weight is very variable, ranging from 3 to more than 15 g 1000 seeds^{-1} (Rachie and Majmudar, 1980). Due to protogyny, the species is highly cross pollinated.

Virtually all commercial pearl millet is sown by seed. Depth of sowing is critical for the establishment of a satisfactory stand (Ferraris, 1973). Sowing depths between 15-50 mm are the most adequate. Sowing rates vary greatly according to sowing techniques. In India, seeds are usually broadcast or drill-sown with animal-drawn implements (Rachie and Majmudar, 1980). Broadcasting seed can increase rates up

to 20 kg ha^{-1}, while drilling in rows reduces rates to less than 4 kg ha^{-1}. For forage production in the Southeastern U.S.A., millet is usually drilled in rows at rates of 10 to 15 kg ha^{-1}.

Cytogenetics and Breeding

Pearl millet is a diploid with a basic chromosome number of seven, showing bivalent pairing of chromosomes during meiosis (Rangaswamy, 1935; Krishnaswamy, 1962). Rau (1929) determined the chromosome number of pearl millet as 2n=14. He indicated that the chromosomes were very large and that the homologous pairs could be easily distinguished.

Pearl millet exhibits a high level of cross pollination due to protogyny (Burton and Powell, 1968). Stigmas remain receptive from 12 to 48 hours according to environmental conditions. Stamens first appear two to three days after stigma exertion, starting near the tip of the partially exerted panicle and proceeding downwards. Time lag between emergence of stigmas and anthers depends primarily on the temperature (Jauhar, 1981). Higher temperatures tend to shorten the time lag.

Organized genetic improvement of pearl millet started in India in the 1920's, though on a modest scale (Jauhar, 1981). Improvement work involved mass selection with emphasis on well-filled, compact, and long panicles, heavy grain, and uniformity in ripening (Krishnaswamy, 1962). African countries followed later, using similar guidelines as those established in India.

Improvement through mass selection may be desirable when the heritability of characters are high. With low heritabilities, where environmental factors are largely responsible for the phenotypic variation, other methodologies would be preferred.

Initial efforts through mass selection in India and Africa were worthwhile, but progress was slow (Jauhar, 1981). Through the years, new methodologies and approaches were used, thus improving the efficiency of breeding programs. After early attempts to assemble genetic stocks at different locations, today the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at Hyderabad, India, holds an extensive germplasm collection for use in breeding programs. ICRISAT is responsible for the collection, maintenance, conservation, documentation, and distribution of pearl millet genetic resources. Breeders can now search for specific traits or genes of interest in this valuable collection. Hanna (1987) discussed the utilization of primary, secondary, and tertiary gene pools to improve pearl millet. The wild, weedy pearl millet subspecies *monodii* and *stenostachyum* (from the primary gene pool) are easily used and are an excellent source for new cytoplasms, stable cytoplasm sterility, pest resistance, hybrid vigor, and other desirable traits. Manipulation and transfer of genes from the secondary and tertiary gene pools is more complex, due to differences in basic chromosome number and ploidy level.

Current breeding efforts are aimed at exploiting heterosis for both grain and forage purposes (Jauhar, 1981; Rachie and Majmudar, 1980). The discovery of cytoplasmic male sterility (CMS) was a key factor in the exploitation of heterosis on a commercial scale. An excellent source of CMS was discovered by Burton (1958), who then released the CMS lines Tift 23A and Tift 18A (Burton, 1965a,b). These lines had been introduced into India in 1961 and were extensively used in hybrid breeding programs (Rachie and Majmudar, 1980). Burton and Athwal (1967) suggested that 3 recessive genes (ms_1, ms_2, and ms_3) in the homozygous state maintained male sterility in cytoplasms A_1, A_2, and A_3, respectively. Corresponding dominant MS genes generally

restored fertility under the homozygous or heterozygous condition. Complete fertility restoration could be prevented by genetic modifiers or environmental factors. Male sterility in pearl millet is discussed in great detail by Jauhar (1981) and Burton (1958). Jauhar (1981) also discussed the possibility of using pearl millet haploids for production of commercial hybrids. Selection at the basic haploid level, induction of chromosome doubling to produce homozygous lines, and subsequent testing of their combining abilities could be a rapid approach to heterosis breeding.

Population sources for elite inbreds have been improved through recurrent selection and reciprocal recurrent selection. Burton and Athwal (1968) described a procedure for the use of reciprocal recurrent selection for the development of improved F_1 hybrids. Creation of synthetic varieties and composites have also been successful in pearl millet. Jauhar (1981) has summarized successful endeavors in these areas.

Development of dwarfs is also desirable for many reasons. Pearl millet and especially its hybrids respond very well to high fertilization rates (Jauhar, 1981). Problems of lodging due to heavy fertilization can be avoided through the manipulation of dwarf genes, thus fully realizing the yield potential of the hybrids. Mechanization of harvests is also easier in dwarf populations. Dwarf stocks were developed at Tifton, Georgia, in the early 1960's. Tift 23DA and 23DB have greatly facilitated the production of dwarf hybrids (Burton, 1967), including interspecific hybrids with other *Pennisetum* species (Diz and Schank, 1991; Hanna, 1981; Schank and Diz, 1991).

Another promising endeavor in the breeding of pearl millet is the utilization of apomixis. The species *Pennisetum squamulatum* Fresen from the tertiary gene pool has been an excellent donor of genes controlling apomixis in pearl millet (Dujardin and Hanna, 1986). The gene(s) for apomixis seem(s) to be located on a single

chromosome (Ozias-Akins et al., 1993). Hanna et al. (1992) have reviewed the transfer of apomixis in *Pennisetum* and the impact it would have in future crop improvement. Obligate apomictic reproduction has not been achieved in any major crop species, but its potential impact on crop production would have global consequences (Ozias-Akins et al., 1993). Serious attempts to transfer the gene(s) for apomixis beyond natural crossing barriers will have to await further elucidation of the inheritance and genetic control of this mode of reproduction (Ozias-Akins et al., 1993).

Elephantgrass

Description, Origin, and Distribution

Pennisetum purpureum Schum. is a perennial grass commonly known as elephantgrass or napiergrass. It is a robust, perennial species which can attain a height of 3-5 m when mature (Brunken, 1977). Morphological features are variable and depend on the genotype evaluated (Bogdan, 1977). Tall elephantgrasses have a cane-like appearance, while dwarfs are more bushy and usually possess a higher leaf-to-stem ratio. Individual plants can produce over 80 tillers, although they generally range between 20 and 35. The inflorescence is a spikelike panicle ranging from 15 to 30 cm long (Silveus, 1933).

High dry matter yields have been reported for elephantgrass. Gardner and Prine (1987) measured 35.9 Mg ha^{-1} yr^{-1} of dry matter for the tall PI 300086 at Gainesville, Florida. Mislevy et al. (1986) reported dry matter yields of 52.2 Mg ha^{-1} yr^{-1} for this same genotype at Ona, Florida. Yields for dwarf cultivars are significantly lower, approximately a third of that of tall types (Sollenberger et al., 1988).

Elephantgrass belongs to the family Gramineae, the subfamily Panicoideae, the tribe Paniceae, the genus *Pennisetum*, and the section Penicillaria. Tropical Africa was identified as the center of origin for this species (Stapf and Hubbard, 1934). It is distributed naturally throughout the forest belt of West Africa, where the rainfall regimes usually exceed 1000 mm (Brunken, 1977). It was introduced into the U.S. in 1913, by the Department of Agriculture (Jauhar, 1981). Today, it is widely distributed throughout tropical and subtropical regions of the world as a forage grass.

Seed Production and Propagation

Elephantgrass inflorescences are classified as panicles, although they have a spikelike appearance. They are cylindrical, erect, and densely flowered, commonly 15 to 30 cm in length (Silveus, 1933). Spikelets are 4 to 6 mm long, with long plumose stigmas and three stamens. Information on elephantgrass seed is rather limited (Jauhar, 1981). Seeds are very small, light, and poor in quality (Schank and Diz, 1991). They are difficult to harvest, shatter very easily, and give rise to weak seedlings, making them inappropriate for seed propagation (Powell and Burton, 1966). Elephantgrass is highly cross-pollinated, so the seeds from a clone are also highly heterozygous and do not breed true. For these reasons, the species is vegetatively propagated throughout the world, typically using whole stems or stem pieces which are planted horizontally in shallow furrows (Sollenberger et al., 1990).

Planting dates vary depending upon location. Plant stems from nurseries for vegetative propagation should be allowed to harden and mature prior to cutting, and then planted with adequate soil moisture, early enough to avoid frosts so that establishing plants can store sufficient underground reserves to survive the winter

(Sollenberger et al, 1988). In areas where frosts are not a problem, adequate soil moisture is of primary concern. In north central Florida, early August through early September is the most appropriate time for planting Mott dwarf elephantgrass (Sollenberger et al., 1988). At this location, stems for planting can be harvested only once from a nursery during the growing season. Vegetative propagation has been the greatest limitation for a more widespread use of elephantgrass. It primarily affects large scale operations or its use in more developed countries, where labor is expensive.

Cytogenetics and Breeding

The somatic chromosome number of elephantgrass was first determined by Burton (1942) and Nishiyama and Kondo (1942) as 2n=28. Fourteen bivalents are usually formed during meiosis, in the absence of multivalent or univalent chromosome pairing (Jauhar, 1968). The subsequent stages of meiosis are regular, resulting in normal isobilateral tetrads, and pollen fertility above 90% (Hanna, 1981; Jauhar, 1981). Elephantgrass is an allotetraploid represented genomically as A'A'BB (Jauhar, 1981). The A' genome is partially homologous to the A genome of pearl millet (which is genomically AA) (Dujardin and Hanna, 1985).

During this century, elephantgrass crop improvement has primarily focused on the evaluation of numerous accessions or plant introductions, worldwide. Due to the existence of large genetic diversity, efforts have been directed towards evaluating this germplasm at different locations. Tcacenco and Lance (1992) have recently studied and discussed the selection of morphological traits for adequate characterization of elephantgrass accessions. Eighty nine characters were evaluated for their usefulness

in identifying accessions. Pereira (1992) recently reviewed the characterization, identification, and classification of elephantgrass varieties. He states that the task of discriminating among varieties can be very difficult. A further complication is that many accessions are renamed by local institutes around the world and so duplications are common within collections (Tcacenco and Lance, 1992).

Intraspecific crosses in elephantgrass with subsequent evaluation of the progeny have been made. The variety 'Merkeron', for example, was selected from a dwarf x tall elephantgrass cross made in 1941 by G.W. Burton at Tifton, Georgia (Bogdan, 1966). Other crosses have been cited more recently in the literature (Hanna and Monson, 1988; Schank, 1986 and 1987; Schank et al., 1989). Because elephantgrass is clonally propagated, a single elite plant can become a cultivar after adequate evaluation over locations and years. This is true for 'Mott' dwarf elephantgrass, the latest elephantgrass cultivar released from the University of Florida (Sollenberger et al., 1989). 'Mott' was selected by W. W. Hanna as a single plant among the selfed progeny of 'Merkeron' elephantgrass (Hanna and Monson, 1988). It was introduced into Florida as 'Tift N75' from Tifton, Georgia in 1977 (Sollenberger et al, 1988). After exhaustive evaluation, it was shown to maintain high forage quality over a much wider range of maturity than is characteristic of most tropical grasses. It is persistent and able to support steer gains of nearly 1 kg day^{-1} throughout summer and early fall (Sollenberger and Jones, 1989). However, because of the costly and labor intensive vegetative propagation, it has not been adopted by farmers in Florida.

Breeding objectives may vary according to the expected use of the future varieties, whether for biomass production (i.e. methane biosynthesis) or forage. Forage breeding objectives may also differ depending on the intended use of the varieties, whether for

direct grazing (dwarf types desired) or other uses such as silage, where intermediate types with higher dry matter production are more desired. Desirable forage characters would include high forage quality, adequate seasonal growth distribution, higher leaf to stem ratio, improved persistence, and high regrowth capacity.

Pearl Millet x Elephantgrass Hybrids

Importance, Distribution, and Utilization

The most widely studied interspecific hybrids in the genus *Pennisetum* are those between pearl millet and elephantgrass (Jauhar, 1981; Muldoon and Pearson, 1979). The first documented man-made hybrid was performed by Burton in 1941 (Burton, 1944). They were later produced in India (Krishnaswamy and Raman, 1949), Hawaii (Van Horn, 1947), South Africa (Gildenhuys, 1950), and Pakistan (Khan and Rahman, 1963). The initial purpose of obtaining this hybrid was to combine the high forage quality, nonshattering seed nature, and resistance to various diseases in pearl millet, with the aggressiveness, perenniality, and rust resistance of elephantgrass. These interspecific hybrids are generally more acceptable as forage plants than elephantgrass (Jauhar, 1981). However, hybrids tend to flower earlier in the season, which is disadvantageous from a forage standpoint. As with elephantgrass, the interspecific F_1 hybrids (2n=3x=21) have to be propagated vegetatively. They are grown commercially in India, Pakistan and Sri Lanka, and have been grown experimentally throughout several tropical and subtropical areas (Muldoon and Pearson, 1979). The lack of good quality seed in commercial quantities, the use of poorly adapted genotypes, and the lack of management expertise, have limited the commercial acceptance and utilization of this hybrid. Economical and reliable establishment techniques will have to be

developed before these forage or biomass interspecific hybrids can be used effectively (Sollenberger et al., 1990).

To date, forage production is the most important use for pearl millet x elephantgrass hybrids. It is usually grown in zero grazing situations (Muldoon and Pearson, 1979), where the forage is cut by hand or machine and carried to the cattle. Other alternative uses involve direct grazing by the cattle, or conserved forage, such as silage or hay (Schank and Diz, 1991). The hybrids also have large potential as biomass energy crops (Schank and Chynoweth, 1993; Schank et al., 1993).

Botanical Description

Pearl millet x elephantgrass hybrids are tall bunchgrasses which usually grow from 1.5 to 5 m in height (Muldoon and Pearson, 1979). They usually produce from 15 to over 70 tillers per plant. The hybrids are commonly non-rhizomatous and develop a shallow fibrous root system. The inflorescence may range from 20 to 40 cm in length and 1.1 to 1.5 cm in diameter. In the triploid F_1 hybrids, stigmas are exerted and appear normal, but anthers are shrivelled and rarely exerted (Hanna, 1981). Most ovules show abortion of all four megaspores (over 99%). Sterility of the F_1 hybrids has been overcome by doubling the chromosome number. These hexaploids show a wide range of pollen viability and seed production (Diz and Schank, 1993). The hybrids tend to resemble elephantgrass more than pearl millet (Muldoon and Pearson, 1979). The relative genetic contribution of the elephantgrass parent is greater (two thirds of the total number of chromosomes), so this would be expected. Additionally, the B genome derived from elephantgrass usually has a dominant effect over the A genome in pearl millet (Gonzalez and Hanna, 1984; Krishnaswamy and Raman, 1949). Some

characters are intermediate between the parental species. There is also considerable variation in the expression of heterosis for different characteristics. Polyploids usually show an increase in the magnitude of many characteristics (Sree Ramulu, 1971). The amphiploids (hexaploids) commonly have thicker stems, broader leaves, and larger panicles when compared to their parental triploids (Jauhar, 1981). Gonzalez and Hanna (1984) observed increases in stem thickness, leaf length, inflorescence length and width, number of spikelets, florets per spikelet, floret length, and pollen grain diameter when comparing triploid and hexaploid isogenic lines.

Seed Production and Propagation

The triploid pearl millet x elephantgrass F_1 hybrid plants are sterile and must be propagated vegetatively. Nevertheless, F_1 seed could be produced commercially because pearl millet and elephantgrass readily cross in the field. Powell and Burton (1966) suggested a commercial seed production scheme, using a male-sterile pearl millet sown annually between perennial rows of elephantgrass. Hand pollination of 'Tift 23A' pearl millet (CMS) with pollen from 'Merkeron' elephantgrass gave excellent seed set with well-filled seeds, but the seed production scheme was not tested in the field. Because of the late flowering of elephantgrass, this scheme would only be possible in areas frost-free until late December (northern hemisphere) (Hanna and Monson, 1980). Aken'Ova and Chheda (1981) tested the procedure in Ibadan, Nigeria, by sowing rows of male-sterile Maiwa pearl millet between rows of 6 elephantgrass ecotypes. They were able to collect 3.17 kg of seed from a small plot, equivalent to 88.5 kg ha^{-1} of hybrid seed. Germination of seed was 45%. Improved seed production will be necessary in order to make this alternative commercially feasible. Aken'Ova and

Chheda (1981) suggested locating seed production in drier pearl millet-growing areas to reduce disease problems. However, elephantgrass would probably need irrigation in these areas. They also suggested manually shaking elephantgrass inflorescences to improve pollen dissemination and seed set. This would be very laborious on a commercial scale.

Sterility of the F_1 hybrids has been overcome by doubling the chromosome number. The resulting hexaploids are highly male and female fertile (Hanna, 1981; Schank and Diz, 1991). Diz and Schank (1991, 1993) have evaluated seed characteristics in several hexaploid genotypes. Large variation in these characteristics were found. Number of seeds per panicle ranged from 0 to over 900; seed set ranged from 0 to 72%; 100-seed weight varied from 0.15 to 0.25 g; and mean seed yield per plant ranged from 5 to 17 g in the seven families evaluated. Direct seeding in the field has been accomplished and has resulted in very good stands. A well prepared seedbed with adequate moisture is required because of the small size of seeds. Adequate soil fertility is also essential for good seedling development. Starter fertilizer placed on the sides of seeded rows is recommended.

To date, seed has not been harvested on a commercial scale. Plants which are not cut or grazed produce panicles at approximately 2.5 to 4.5 m in height, from the end of September to mid-November, at Gainesville, Florida (Diz and Schank, 1993). In order to facilitate mechanical seed harvesting, panicle height and plant biomass need to be reduced, while seed production is maintained. This may be achieved through defoliation management, which would allow the dual use of the stand for forage and seed.

Cytogenetics and Breeding

Pearl millet x elephantgrass F_1 hybrids are sterile triploids with 21 chromosomes (2n=3x=21). During meiosis they usually form 7II and 7I (Khan and Rahman, 1963; Krishnaswamy and Raman, 1954; Sree Ramulu, 1971). The bivalent formations arise from the synapsis between the pearl millet A genome and the elephantgrass A' genome. Other chromosomal associations have also been observed (Jauhar, 1981). Due to meiotic irregularities, the triploid hybrids are almost completely sterile. Sterile pollen and abortion of all four megaspores are usually observed (Hanna, 1981; Jauhar, 1981).

Hexaploids have been obtained by treating the triploid hybrids with colchicine (Gildenhuys and Brix, 1964; Gonzalez and Hanna, 1984; Krishnaswamy and Raman, 1949; Hanna, 1981), severe pruning (Jauhar and Singh, 1969), and tissue culture (Rajasekaran et al., 1986). Cytogenetics of these hexaploids (2n=6x=42) differ greatly from that of the triploids. Hexaploids usually form 21 bivalents during meiosis, with multivalents usually absent or infrequent (Krishnaswamy and Raman, 1954; Jauhar and Singh, 1969). They behave meiotically like typical allohexaploids. This is due to the preferential pairing between the A-A, A'-A', and B-B genome chromosomes (Jauhar, 1981). The partial homology between the A and A' genomes is indicated by the allosyndetic pairing in the triploid and the low frequency of multivalents in the amphiploid. Megasporogenesis and embryo sac development are typically sexual (Hanna, 1981).

Pearl millet and elephantgrass cross spontaneously under natural conditions, by virtue of their protogynous nature (Burton and Powell, 1968; Muldoon and Pearson, 1979). It is preferable to use pearl millet as the female parent in crosses for several

reasons: a) larger and higher quality seed is produced; b) seed shattering is absent or minimal; and c) it is easier to identify hybrids at the seedling stage (Jauhar, 1981). Nevertheless, crosses can also be obtained by using pearl millet as the male parent (Krishnaswamy and Raman, 1956). With the development of cytoplasmic male-sterility in pearl millet (Burton and Powell, 1968), the hybridization process was simplified by eliminating the need to distinguish between hybrid and inbred seedlings.

Although several superior pearl millet x elephantgrass triploid hybrids have been produced in different countries, they have not been adopted on a wide scale because they are completely sterile (Jauhar, 1981). Jauhar suggested that for easy distribution to farmers, superior, fertile, seed-producing hexaploid hybrids or derivatives would need to be developed. Under the guidance of Dr. S. C. Schank, efforts are currently underway at the University of Florida to develop hexaploid hybrid varieties. Breeding objectives have focused on increasing forage nutritive value, dry matter production, seed production, and persistence (Schank and Diz, 1991).

The *Pennisetum* hexaploid population at the University of Florida originated from a series of crosses involving the cytoplasmic male-sterile inbred Tift 23DA (dwarf) pearl millet, Mott dwarf elephantgrass, and the tall pearl millet x elephantgrass hexaploid hybrids MN3 and MN33 (2n=6x=42) obtained from Dr. W. W. Hanna, USDA-ARS, Tifton, Georgia. MN3 and MN33 were derived from the crosses 23DA x N13 and 23DB x N9, respectively. Both hybrids were treated with colchicine to double the chromosome number. The population was generated as follows: In 1986, Tift 23DA was crossed to Mott and triploid progeny were obtained. Selected plants were then grown in tissue culture (Rajasekaran et al., 1986), and through this process, two hexaploid plants were obtained. One of these plants (P3) was then crossed to MN3.

The following year, hybrids of P3 x MN3 were crossed to MN33 which contains restorer genes and hence, male fertility was improved. Mass selection for biomass, persistence, and fertility during two years resulted in the population on which this study was based.

CHAPTER 3
SEED RELATED CHARACTERISTICS IN PEARL MILLET X ELEPHANTGRASS HYBRIDS AS INFLUENCED BY DEFOLIATION MANAGEMENT

Introduction

Elephantgrass is a high yielding forage and biomass grass which has low natural seed production and very poor seed quality. For these reasons, it is propagated vegetatively throughout the world. However, very productive cultivars such as the persistent and high quality dwarf cultivar "Mott", released in Florida in 1989, are not being used commercially in the U.S. because of the high cost and labor required for establishment (Sollenberger and Jones, 1989; Schank and Diz, 1991). A seeded, high-quality elephantgrass hybrid has been obtained through hybridization with pearl millet and further breeding, which may solve this problem (Schank and Diz, 1991; Diz and Schank, 1991). The hybrid is a hexaploid ($2n=6x=42$) and its development has been described elsewhere (Schank and Diz, 1991; Diz and Schank, 1993). A problem which remains to be solved prior to widespread use of the hybrids is mechanical seed harvesting. Plants which are not cut or grazed produce panicles at approximately 2.5 to 4.5 m in height, from the end of September to mid-November, at Gainesville, Florida. In order to mechanically harvest seeds, panicle height and plant biomass need to be reduced, while seed production is maintained. This may be achieved through defoliation management, which would allow the dual use of the stand for forage and seed.

Numerous experiments have been conducted on the effects of defoliation on winter cereal crop seed production. In general, certain plant responses can be expected: a) Under poor weather and fertility conditions, yield losses can be expected when winter cereal crops are grazed in the vegetative stage (Kilcher, 1982). b) Grazing cereal crops during the culm elongation stage greatly reduces seed yield due to removal of growing points (Holliday, 1956; Winter and Thompson, 1987), therefore timing of cutting or grazing is crucial. c) Compensation of the plant to increase leaf area and plant biomass after grazing is dependent on stage of vegetative development as well as severity of defoliation (Christiansen et al., 1989). d) Moderate grazing can be effective in using green fodder without significant loss in subsequent grain yield (Christiansen et al., 1989). e) Increases in grain yield due to grazing are usually attributed to a removal of forage which prevented lodging (Holliday, 1956; Aldrich, 1959); and f) Grazing often reduces plant height and delays flowering (Dann et al., 1983; Winter et al., 1990). These general responses may apply to the pearl millet x elephantgrass hybrids.

Relative to tropical grasses, Scheffer et al. (1985) found a linear decrease in seed yield with increasing number of cuts in pearl millet, primarily due to a reduction in the number of panicles ha^{-1}. Nevertheless, seed quality, measured as percent germination and seedling vigor, was not affected by cutting treatments. In the short-day tropical grass *Paspalum plicatulum* Michx., Stür and Humphreys (1987) found that late cutting delayed floral initiation and reduced tiller length, spikelets $raceme^{-1}$, percent seed set, and seed yield $inflorescence^{-1}$, relative to earlier defoliation. In *Andropogon gayanus* Kunth., Andrade and Thomas (1981) found that removal of forage during the first half of the growing season reduced the height of plants and improved seed production.

However, swards cut later flowered profusely but the reduced leaf canopy led to smaller inflorescences and greatly reduced seed yield. In other species, cutting or grazing can promote vegetative expansion of axillary buds, which may result in greater inflorescence density (Humphreys and Riveros, 1986). However, increased tillering is not always allied with greater inflorescence density. Mishra and Chatterjee (1968) found that repeated cutting stimulated tillering in *Pennisetum polystachyon* (L.) Schult. and *Andropogon gayanus* Kunth, but decreased tiller fertility and seed production. When studying defoliation effects on seed production and related traits, we must be aware of interactions among genotypes, defoliation treatments, and years. These may be responsible for inconsistent results or even contradictory results. To predict plant responses with confidence, repeated local experience is essential.

In tropical grasses, compensatory effects among seed yield components are common (Humphreys and Riveros, 1986). Path-coefficient analysis (Wright, 1921) has been useful in determining the importance of seed yield components and their correlational structure in a number of crops. Each correlation coefficient between a predictor variable and the response variable is partitioned into its component parts: the direct effect or path coefficient for the predictor variable (a standardized partial regression coefficient) and the indirect effects, which involve the product of a correlation coefficient between two predictor variables with the appropriate path coefficient in the path diagram (Li, 1975). By determining the interrelationships among seed yield components, a better understanding of the effect which defoliation has on each component and their influence on seed yield can be attained.

The objectives of this study were a) to evaluate the effects of three defoliation treatments on the height of panicles produced, date of flowering, seed yield

components, seed yield plant^{-1}, seed germination, and plant survival in four pearl millet x elephantgrass amphiploid hybrid genotypes; b) to detect interactions among genotypes, treatments, and years; and c) to evaluate the correlations and compensatory effects among seed yield components and their effects on seed yield through the use of path-coefficient analysis.

Materials and Methods

This experiment was conducted at the Dairy Research Unit of the University of Florida, Gainesville, Florida (29° 48'N lat.), during 1991 and 1992. The soil at the experimental site is classified as a Mulat sand; a sandy, siliceous, thermic Arenic Ochraquult. Total rainfall for 1991 and 1992 at the Gainesville airport station was 1295 and 1379 mm, respectively.

Four genotypes and three cutting treatments were evaluated over two years. The genotypes selected (45s, 128s, 131s, and 140s) had the following characteristics: intermediate to tall (3 to 4.5 m at maturity); high number of tillers (25 to 60); relatively early flowering (end of September to mid-October); and high seed production. The three cutting treatments were a) no cuts; b) cut two times per year; and c) cut three times per year. Plants were cut to a stubble height of 30 cm, with a 6-wk interval between successive cuttings. In 1991, the cuts took place on 26 June, 5 Aug., and 15 Sept. In 1992, the cuts were on 23 June, 2 Aug., and 13 Sept. The experimental design consisted of a randomized complete block, with 3 replications. Within a block, each genotype - cutting treatment combination contained 4 plants derived from cuttings. Plants were spaced 2.7 m within a row and 1.35 m between rows. Plants were started in the greenhouse from multiple cuttings and then transplanted into the

field on 25 Apr 1991. During 1991, fertilizer was applied in four split applications (25 Apr, 21 June, 5 Aug, and 5 Sept), for a total of 290-47-93 kg ha^{-1} of $N\text{-}P_2O_5\text{-}K_2O$. Four applications were implemented that year after plant chlorosis became apparent in plants later in the season, due to high nitrogen leaching. In 1992, fertilizer was applied in three split applications (10 Apr, 25 May, and 25 July) for a total of 270-68-136 kg ha^{-1} of $N\text{-}P_2O_5\text{-}K_2O$. Irrigation was not applied in this experiment.

Morphological and fertility characteristics measured included height of plant to top of inflorescences, days to flowering (from 25 Apr.), seed yield components (primary panicles $plant^{-1}$, secondary panicles $tiller^{-1}$, seeds $panicle^{-1}$, and 100-seed weight), seed yield $plant^{-1}$, and germination percentage. For secondary panicles $tiller^{-1}$, four tillers per plant were counted and averaged for analysis. Seed yield was obtained by harvesting and threshing five primary panicles per plant. The yield obtained was divided by five to determine seed yield $panicle^{-1}$ and then multiplied by primary panicles $plant^{-1}$ to estimate seed yield $plant^{-1}$. Seed yield $panicle^{-1}$ was divided by the 100-seed weight and multiplied by 100 to estimate seeds $panicle^{-1}$. Germination was evaluated in petri dishes containing moist filter paper, maintained at 30°C in a germinator for 8 d. One hundred seeds per plant were germinated.

Plants were scored for survival (dead or alive) and vigor (on a 1 to 10 scale, where a 1= 1 or 2 tillers, 10-15 cm tall; and a 10= >25 tillers, >50 cm tall) early in the growing seasons of 1992 and 1993, to assess the effects of defoliation on these characteristics. Additionally, in 1992, two plants were sampled from each genotype - treatment combination within a block, by removing a tiller for culm dissection on the 3, 13, and 24 Sept. The position and size of the immature primary panicle within the culm was determined. This was important for evaluating when cutting could reduce seed

production by removing immature panicles prior to their emergence.

Statistical analysis: Data were analyzed as a randomized complete block in a 4x3x2 factorial arrangement of treatments (genotypes, defoliation treatments, and years, respectively). Levels of these three factors were considered fixed effects in the analysis of variance. Because the genotype x year interactions were significant for all the characteristics measured, 1991 and 1992 data were analyzed separately. Whenever the genotype x defoliation interaction was significant, the analysis was carried out on a per genotype basis. Treatment means were differentiated using Fisher's protected least significant difference. Path analyses were carried out according to the causal relationships portrayed in Fig. 3.1. Since year effects were significant for all the components involved in the paths, a separate path analysis was carried out for each defoliation x year combination, for a total of six analyses. The Statistical Analysis System (SAS, Institute Inc., 1985) was used to compute phenotypic correlation coefficients and standardized multiple regression analyses. Through the multiple regression analyses, standard partial regression coefficients (path coefficients) were obtained. Indirect path coefficients were calculated as described by Li (1975) and Williams et al. (1990).

Results and Discussion

Greater leaching of nitrogen was apparent in 1991 through deficiency symptoms (chlorosis) on the lower leaves of plants. For this reason, four fertilizer applications instead of three were needed that year, and plants were fertilized later in the season compared to 1992. Since N fertilization is one of the most important factors affecting seed production (Humphreys and Riveros, 1986), this information will be relevant when

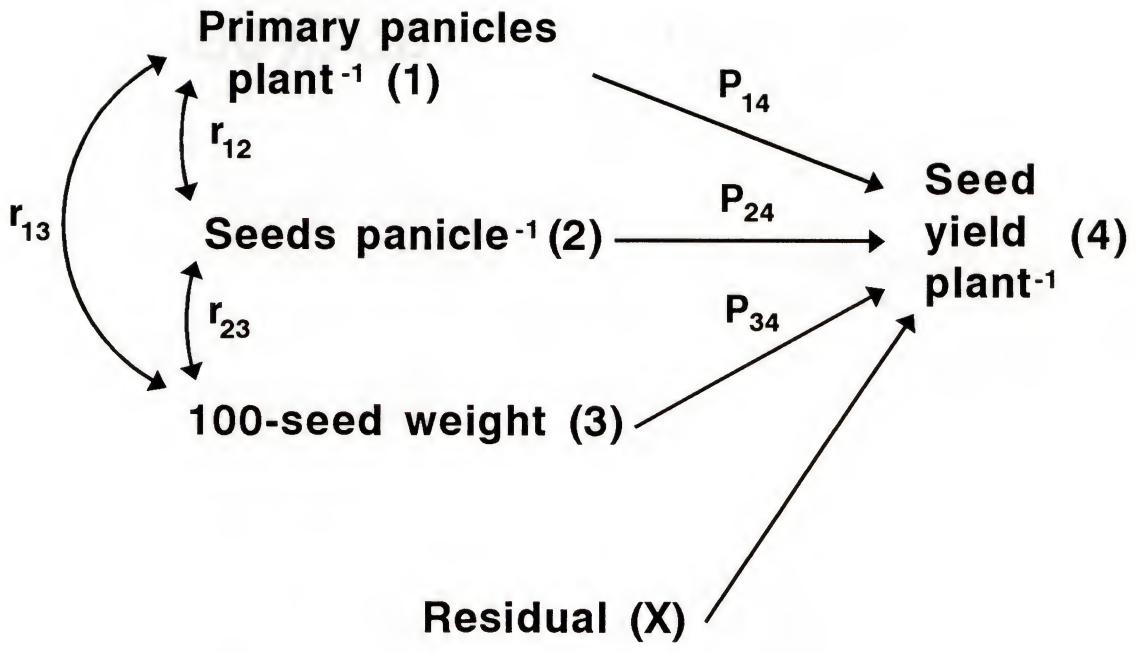

Fig. 3.1. Path diagram showing direct and indirect effects of three seed-yield components on seed yield plant^{-1} in pearl millet x elephantgrass hybrids. Unidirectional arrows represent path coefficients (direct effects) while bidirectional arrows represent correlation coefficients between yield components.

evaluating the results.

Significant defoliation (D) and genotype (G) effects, and DxG interactions were found for all the characteristics in the combined year analyses and individual year analyses, except for germination percentage. Only defoliation effects were significant in the combined year analysis for germination. Year (Y) differences were detected for all the characteristics except secondary panicles tiller^{-1}. The DxGxY interaction was significant for all characteristics except secondary panicles tiller^{-1} and 100-seed weight. However, for these two traits, the GxY interaction was significant. Due to the significance of the interactions mentioned, most characteristics were analyzed on a per-level basis for the factors in question. The linear effects of defoliation accounted for 18 to 90% of the total variation for the characteristics in 1991, and 18 to 96% in 1992.

Plant Height

Linear effects of defoliation on plant height contributed 88 and 96% of the variation in sums of squares for 1991 and 1992, respectively. For both years, the highly significant GxD interaction indicated that the response to defoliation was not the same for all genotypes in the study. In Tables 3.1 and 3.2, the overall genotype means for each defoliation level are indicated for 1991 and 1992, respectively. The percent reduction in height when cut two or three times is also indicated. In 1991, the reduction in height with two cuts was slightly over 1 m, and with three cuts, an additional 0.90 m, approximately. This reduction in height would make direct mechanical harvesting possible, as long as seed production were not greatly affected.

Table 3.1. Overall genotype means for the characteristics evaluated in 1991, showing percent change when cut two or three times, compared to uncut plants.

Defoliation treatment	Height		Days to flowering		Primary panicles plant^{-1}		Second. panicles tiller^{-1}		Seeds panicle^{-1}		100-seed weight		Seed yield plant^{-1}		Germination	
cuts	m	%†	d	%†	no.	%†	no.	%†	no.	%†	mg	%†	g	%†	%	%†
0	3.45		169		30.8		5.0		565		235		38.2		70.3	
2	2.36	-32	175	+4	31.7	+3	1.2	-76	593	+5	256	+9	48.9	+28	65.0	-8
3	1.48	-57	184	+9	18.1	-41	0.0	-99	213	-62	205	-13	8.7	-77	28.1	-60
LSD 0.05	0.05		1		2.0		0.2		50		9		4.3		4.5	

† Percentage change as compared to uncut plants.

Table 3.2. Overall genotype means for the characteristics evaluated in 1992, showing percent change when cut two or three times, compared to uncut plants.

Defoliation	Height		Days to flowering		Primary panicles plant^{-1}		Second. panicles tiller^{-1}		Seeds panicle^{-1}		100-seed weight		Seed yield plant^{-1}		Germination	
cuts	m	%†	d	%†	no.	%†	no.	%†	no.	%†	mg	%†	g	%†	%	%†
0	4.21		165		46.2		5.3		346		190		29.6		70.2	
2	1.95	-54	180	+9	23.3	-50	1.4	-73	307	-11	204	+7	16.7	-44	70.5	‡
3	1.01	-76	202	+22	4.1	-91	0.0	-100	80	-77	156	-18	0.6	-98	55.2	-21
LSD 0.05	0.08		2		2.9		0.4		44		10		4.4		6.1	

† Percentage change as compared to uncut plants.

‡ Less than 1% difference.

With plants cut twice, a combine sickle bar could cut at 1.5 m and still avoid the majority of the leafy biomass. If a brush harvester were used, the spinning brush would have to be placed higher, which is possible. In 1992, uncut plants grew taller because of a well-established root system from the previous year, and they started growing earlier that season. However, defoliated plants in 1992 were shorter than defoliated plants in 1991. The different timing of fertilizer applications for both years, as well as possible competition from the larger uncut plants in 1992 could have caused this. For these reasons, percent reduction in height was greater in 1992 than 1991. In Table 3.3, the mean height for each GxDxY combination is shown. Differences in height among defoliation treatments were significant in both years for all genotypes.

Days to Flowering

Linear effects of defoliation contributed 74 and 83% of the variation in days to flowering for 1991 and 1992, respectively. As with height, the response to defoliation was not the same for all genotypes in the study, indicated by the highly significant GxD interaction. On average, there was a 6 d delay in flowering with two cuts and 15 d with three cuts in 1991; and 15 d with two cuts, 32 d with three cuts in 1992 (see Tables 3.1 and 3.2). The lower supply of assimilates to the inflorescences due to the decrease in leaf area would probably be responsible for the delay (Humphreys and Riveros, 1986). Additionally, if reproductive apices were removed through defoliation, new reproductive apices would have to be induced and would delay flowering. This delay in flowering is of utmost concern because it shifts flowering time further into cool autumn nights, which could affect seed production. Delayed flowering is also a problem in areas where early freezes take place, such as Gainesville, Florida. On

Table 3.3. Pearl millet x elephantgrass genotype means for plant height, days to flowering, seed yield components, seed yield, and germination for the three defoliation levels in 1991 and 1992.

Genotype	Defol. Trt.†	Height	Days to flowering	Primary panicles plant^{-1}	Second. panicles tiller^{-1}	Seeds panicle^{-1}	100-seed weight	Seed yield plant^{-1}	Germin.‡
	cuts	m	d	---------- no.----------			mg	g	%
				1991					
45s	0	3.47	174	25.0	3.9	692	193	33.3	69.9
	2	2.48	177	25.8	0.9	538	208	29.2	55.0
	3	1.56	186	13.8	0.0	256	166	6.5	28.6
	LSD 0.05	0.09	2	2.1	0.3	97	16	5.4	13.2
128s	0	3.60	162	24.8	6.1	406	289	28.5	63.2
	2	2.48	172	31.6	1.6	673	314	66.7	69.3
	3	1.54	183	20.8	0.0	145	231	6.9	31.7
	LSD 0.05	0.06	2	4.0	0.3	105	22	9.6	8.6
131s	0	3.73	168	28.9	4.7	751	252	54.9	74.1
	2	2.59	174	30.1	1.7	935	283	80.2	71.1
	3	1.79	183	20.1	0.1	271	202	12.0	22.0
	LSD 0.05	0.09	1	2.4	0.3	114	19	9.1	6.4
140s	0	3.01	172	43.3	5.5	383	213	34.4	72.7
	2	1.90	177	39.3	0.5	225	220	19.5	64.6
	3	1.03	186	17.8	0.0	97	188	4.3	45.0
	LSD 0.05	0.12	2	5.0	0.3	103	9	7.9	7.8
				1992					
45s	0	4.08	175	41.3	4.6	477	181	35.6	72.5
	2	1.86	181	20.7	1.2	252	177	9.3	75.5
	3	0.99	203	3.1	0.0	98	154	0.6	61.2
	LSD 0.05	0.13	3	2.8	0.5	35	8	4.0	13.2
128s	0	4.49	154	39.1	6.8	190	212	15.7	68.0
	2	1.95	174	22.7	2.0	330	239	19.1	64.8
	3	1.03	196	5.8	0.0	46	143	0.4	50.9
	LSD 0.05	0.13	2	4.0	0.6	61	16	5.3	13.1
131s	0	4.45	165	45.2	3.8	577	204	53.2	75.8
	2	2.20	180	25.3	1.5	494	236	31.4	75.2
	3	1.10	205	4.8	0.0	123	178	1.2	59.0
	LSD 0.05	0.14	2	3.3	0.5	111	15	11.3	11.5
140s	0	3.83	168	59.1	5.9	141	164	13.7	64.8
	2	1.76	186	24.6	1.0	139	162	5.9	66.4
	3	0.93	206	2.0	0.0	18	138	0.1	49.5
	LSD 0.05	0.15	4	9.5	0.7	84	15	7.3	15.3

†: Defoliation treatment.
‡: Germination percentage.

average, flowering of plants cut three times in 1992 took place two weeks prior to the date when 50% of the years have an earlier freeze at Gainesville, Florida (27 Nov.). Mean days to flowering for each GxDxY combination is shown in Table 3.3. Genotype differences were evident, with genotypes 128s and 131s being the earliest flowering. Differences among defoliation treatments were significant for all genotypes in 1991 and 1992.

Seed Yield Components

Linear effects of defoliation on primary panicles plant^{-1}, secondary panicles tiller^{-1}, seeds panicle^{-1}, and 100-seed weight accounted for 43-82%, 90-81%, 25-33%, and 18-22% of the total variation for 1991-1992, respectively. Linear effects were consistently higher for secondary panicles tiller^{-1}. Factors other than defoliation influenced the variability encountered in primary panicles plant^{-1}, seeds panicle^{-1}, and 100-seed weight to a greater extent. Percent change due to defoliation (compared to uncut plants) was also greatest for secondary panicles tiller^{-1} (Tables 3.1 and 3.2). The decreased supply of assimilates in defoliated plants and their later flowering drastically reduced secondary panicles tiller^{-1}. Nevertheless, for commercial seed production, this component may not be important. Direct mechanical harvesting would probably emphasize seed production from primary panicles.

Overall responses for primary panicles plant^{-1} was different in both years. In 1991, plants with two cuts had higher primary panicles plant^{-1} than uncut plants in all but one genotype, 140s (Table 3.3). The removal of apices promoted a greater vegetative expansion from axillary buds, which resulted in greater inflorescence density. Plants cut three times reduced this component in 1991 by an average 41%, thus drastically

reducing seed production potential. In 1992, uncut plants had more tillers and primary panicles than in 1991 (Tables 3.1 and 3.2). Plants defoliated two and three times reduced primary panicles by an average of 50 and 91%, respectively. This difference compared to 1991 was probably due primarily to the differences in fertilizer timing. In 1991, plants received two applications after being cut twice (5 Aug), while no fertilizer was applied after 25 July in 1992. Competition from the larger uncut plants in 1992 could have also played a role.

Seeds panicle^{-1} were lower in 1992 than 1991 for all genotype x defoliation treatment combinations (Table 3.3). The differences in fertilizer application and other environmental differences between years were probably responsible for this. In 1991, the overall genotype mean for seeds panicle^{-1} increased 5% with 2 cuts and decreased 62% with 3 cuts, compared to uncut plants (Table 3.1). Genotypes 128s and 131s were responsible for the increase in mean seeds panicle^{-1} of plants cut two times in 1991 (Table 3.3). Genotype 128s showed this same pattern in 1992. These genotypes, especially 128s, were the ones which flowered the earliest. Because these hybrids are protogynous and cross-pollinated in nature, there may have been insufficient pollen for adequate pollination and seed set in the earlier flowering uncut plants. In individual panicles, stigmas are receptive approximately 3 to 5 days prior to anthesis. Genotypes 128s and 131s cut twice, delayed flowering and stigmas were receptive when pollen concentration in the air was greater. This could account for the greater number of seeds panicle^{-1} in plants cut twice. In 1992, mean seeds panicle^{-1} was reduced 11 and 77% with two and three cuts, respectively (Table 3.2). Overall, two cuts did not affect seeds panicle^{-1}, but three cuts reduced it very significantly. The

later flowering with cooler nights and the decreased supply of assimilates from smaller plants probably caused this.

As often happens with other agronomic crops, 100-seed weight was the component least affected by defoliation. Seed weight was higher for all genotypes in 1991, probably due to the difference in fertilizer timing, with later applications favoring higher seed weight. In 1991, the 100-seed weight of all genotypes cut two times was greater than that of uncut plants, although only significant in the early flowering genotypes 128s and 131s (Table 3.3). These two genotypes also had a greater seed weight when cut two times in 1992, compared to uncut plants. Environmental differences during the seed filling period (it was drier during the delayed flowering of the 128s and 131s plants cut twice), and a possible defoliation-induced modification of the source-sink assimilate relationships within the plants could have produced this result. In summary, seed weight was not reduced when plants were cut twice. Seed weight of plants cut three times was reduced in all cases, with an average 13 and 18% decrease for 1991 and 1992, respectively (Tables 3.1 and 3.2). This lower seed weight in plants cut three times was greatly reflected in the germination of seeds, which will be discussed later.

Seed Yield Plant^{-1}

Seed yield plant^{-1} was lower in 1992, primarily due to a reduction in seeds panicle^{-1} and weight of seeds (Tables 3.1 and 3.2). The different environmental conditions and the difference in timing of fertilizer applications were probably responsible for this. In 1991, plants cut two times had a higher overall mean seed yield than uncut plants (Table 3.1), because of higher seed yields in genotypes 128s and 131s (Table 3.3). For these two genotypes, all seed yield components had increased when cut two times

(except secondary panicles tiller^{-1}, which were not taken into account for calculating seed yield plant^{-1}). Seed yield was drastically reduced in plants cut three times due to a decrease in all yield components (Table 3.1). The component most affected was seeds panicle^{-1}. In 1992, only genotype 128s cut twice yielded more than the uncut plants. In the other genotypes, there was an important reduction in seed yield plant^{-1}, primarily due to a reduction in primary panicles plant^{-1} (Table 3.3). Plants cut three times in 1992 yielded very poorly, with important reductions in all seed yield components (Table 3.2).

Germination

Linear effects of defoliation accounted for 70 and 18% of the variation in germination for 1991 and 1992, respectively. The GxD interaction was significant only in 1991, revealing that defoliation effects differed according to genotype. In Tables 3.1 and 3.2, the overall genotype means for each defoliation level are shown for 1991 and 1992, respectively. There were no differences in germination percentage between uncut plants and plants cut twice. However, three cuts reduced germination 60% in 1991 and 21% in 1992. The lower quality of this seed was reflected by the reduction in 100-seed weight, which was mentioned previously. In Table 3.3, the mean germination for each GxDxY combination is shown. The reduced germination in plants cut 3 times was observed in all genotypes.

Removal of Immature Panicles due to Cutting

By evaluating the size and position of the immature primary panicle within the culm at different dates, it was possible to determine when the meristems began reproductive differentiation and when cutting would accidentally eliminate these immature panicles.

Table 3.4 shows the mean immature panicle length and its elevation from the soil surface (within the culm) on 3, 13, and 23 Sept., for the four genotypes evaluated. On 3 Sept., immature panicles or undifferentiated meristems on all uncut genotypes were well above soil-level, so cutting would eliminate these meristems or immature panicles. The earliest flowering genotype, 128s, was already induced for panicle elongation, with a mean immature panicle length of 19 mm (uncut plants). For genotype 131s, only a few culms were induced, with the panicles just starting to elongate. Uncut plants from genotypes 45s and 140s did not have induced panicles, as well as all plants which had been previously cut, regardless of genotype. Ten days later (13 Sept.) all uncut plants had elongating panicles. Genotype 45s still had several culms per plant where panicle elongation had still not begun. Genotypes 128s, 131s, and 140s, which had been cut twice, were also elongating their panicle primordia. These immature panicles were removed that same day on those plants which were cut for a third time at a height of 30 cm. This removal of reproductive apices would greatly decrease seed yield potential in those plants cut a third time, and delay flowering further into cool autumn nights, and the possibilities of an early freeze. This would explain the low seed yields obtained for plants cut three times in 1991 and 1992. Ten days later (23 Sept.), genotype 45s cut twice also began elongating its panicle primordia. Uncut plants from genotype 128s had their panicles practically fully developed, and they began exerting from their flag leaves. Data for plants cut three times was not available on that date, since new tillers were just starting to arise from newly induced buds.

Data for 1991 was not collected, but because plants cut twice flowered a few days earlier in 1991 compared to 1992 for all genotypes (see Table 3.3), the third cut on 15 Sept. 1991, most likely removed elongating panicles as in 1992. This explains the great reduction in seed yield for plants cut three times in both 1991 and 1992.

Table 3.4. Mean immature panicle length (L) and elevation (E) from soil surface (within culm) on three different dates in September 1992, for all genotype x defoliation treatment combinations.

Defoliation treatment	GENOTYPES							
	45s		128s		131s		140s	
	L	E	L	E	L	E	L	E
cuts	mm	m	mm	m	mm	m	mm	m
Date 1 (3 Sept)								
0	0	1.43	19	2.19	1	1.91	0	1.63
2	0	0.35	0	0.39	0	0.36	0	0.36
3	0	0.34	0	0.37	0	0.35	0	0.35
Date 2 (13 Sept)								
0	1.5	1.58	278.0	2.64	11.5	2.30	8.7	1.98
2	0	0.36	1.3	0.48	0.8	0.41	0.5	0.40
3	0	0.36	0.7	0.45	0.3	0.40	0.3	0.38
Date 3 (23 Sept)								
0	13.2	1.80	371.0	3.85	177.3	2.80	198.5	2.41
2	0.5	0.42	47.5	0.90	2.5	0.50	1.8	0.43
3	-	-	-	-	-	-	-	-

Survival and Vigor

Pearl millet x elephantgrass hybrids are perennial, but both genotype and management practices affect their survival. Persistence is very desirable for seed production since seed could be harvested from the same field year after year. In a study reported by Macoon (1992), survival of different genotypes ranged from 7 to 46% across defoliation treatments. In another study, the hybrids did not persist well under the cutting treatments imposed, with percent survival ranging from 10 to 32% (Spitaleri, 1992). Differences in survival due to genotype have not been studied adequately, although they probably show greater variation than differences in survival due to management. The genotypes selected for this study had previously been classified as possessing good persistence and adequate vigor in the year following establishment. In Table 3.5, mean survival and vigor scores taken early in the growing seasons of 1992 and 1993 are shown for the different defoliation treatments. Survival was good in both years (88-100%), probably due to the genotypes used. Letting the plants set seed and accumulate carbohydrate reserves in rhizomes at the end of the season also favored persistence. Plants cut twice showed no difference in survival compared to uncut plants, while survival of plants cut three times was reduced somewhat. Differences in early plant vigor for the defoliation treatments were not significant in 1992, but appeared significant in 1993. Continuous cutting year after year could weaken the plants and reduce their vigor, although more prolonged studies would be needed to determine this.

Table 3.5. Mean survival and vigor scores taken early in the growing seasons of 1992 and 1993. Means for the three defoliation treatments are shown.

	1992		1993	
Defoliation	Survival	Vigor†	Survival	Vigor†
Cuts	%	Score	%	Score
0	98	6.0	100	8.4
2	100	6.0	98	5.2
3	94	5.3	88	3.5
LSD(0.05)		NS		0.5

† Vigor score: 1 to 10 scale, where a 1= 1 or 2 tillers, 10-15 cm tall; and a 10= >25 tillers, >50 cm tall.

Path-Coefficient Analyses

Due to defoliation, the correlational structures among seed yield components and seed yield plant^{-1} were probably altered. Uncut plants in both years and plants cut twice in 1991 had high seed yields plant^{-1} (Tables 3.1 and 3.2). In the interpretations that follow, these treatments were considered high-yielding situations. Plants cut twice in 1992 and three times in both years had low seed yields plant^{-1}, and were considered low-yielding situations. In these latter cases, some or all yield components were reduced by defoliation compared to uncut plants.

Phenotypic correlation coefficients for seed yield components and seed yield plant^{-1} are presented in Table 3.6. Negative correlations among seed yield components can be interpreted as compensation among these components. The supply of growth factors which stimulate one yield component will be equilibrated by a reduction in another yield component, if competition reaches a point where a shortage of a growth factor is induced (Humphreys and Riveros, 1986). This is common in tropical grasses and many seed crops. Negative correlations among seed yield components were found in the high-yielding situations (uncut plants in both years and plants cut twice in 1991) (see Table 3.6). In all cases there was a negative correlation between primary panicles plant^{-1} and seeds panicle^{-1}, although it was not significant for uncut plants in 1992 (-0.25). The correlation between primary panicles plant^{-1} and 100-seed weight was also negative in all high-yielding situations. It was not significant in 1991 plants cut twice (-0.08). The correlation between seeds panicle^{-1} and 100-seed weight in the high-yielding situations was more erratic. It was not significantly different from zero in two cases (1991 and 1992 uncut plants), showing basically no compensation between these components; but it was highly significant and positive in the other high-yielding

Table 3.6. Phenotypic correlation coefficients among seed yield components and seed yield plant^{-1} for each defoliation treatment in 1991 and 1992.

Seed yield components	1991			1992		
	Seeds panicle^{-1}	100-seed weight	Seed yield plant^{-1}	Seeds panicle^{-1}	100-seed weight	Seed yield plant^{-1}
			NO CUTS			
Panicles plant^{-1}	-0.46**	-0.30*	-0.01	-0.25	-0.51**	-0.02
Seeds panicle^{-1}		-0.14	0.78**		0.25	0.93**
100-seed weight			0.14			0.28
			TWO CUTS			
Panicles plant^{-1}	-0.36*	-0.08	-0.03	0.40**	0.26	0.63**
Seeds panicle^{-1}		0.60**	0.91**		0.75**	0.94**
100-seed weight			0.78**			0.75**
			THREE CUTS			
Panicles plant^{-1}	-0.01	0.46*	0.46*	0.03	0.39	0.53**
Seeds panicle^{-1}		0.06	0.82**		0.48*	0.72**
100-seed weight			0.48**			0.77**

*,** Significant at the 0.05 and 0.01 probability level, respectively.

situation (two cuts, 1991). This lack of compensation between seeds panicle^{-1} and 100-seed weight is not common in crops where the seed harvest index is relatively high. However, in pearl millet x elephantgrass hybrids, where the seed harvest index is very low, positive phenotypic and genetic correlations between these two components were previously found (described later in Chapter 4).

In the low-yielding situations (plants cut twice in 1992 and three times in both years), a different correlational structure among seed yield components was found (Table 3.6). Correlations among components were either not significantly different from zero or were positive. Negative correlations, indicating compensatory effects among seed yield components, were not apparent. Changes in the assimilate source-sink relation were probably responsible for this. There was an important reduction in the assimilate supply of these plants cut two or three times, but the demand for assimilates was also greatly diminished, probably more so than the supply. For this reason, competition among components was not intense and compensatory effects were not found. Another interesting observation was the attenuation of relationships with other components for those components most affected by defoliation. For example, seeds panicle^{-1} was the component most affected in plants cut three times in 1991 (see Table 3.1). The correlations between this component and the other two (panicles plant^{-1} and 100-seed weight) were the lowest, and not different from zero (Table 3.6). Plants cut two or three times in 1992 showed a large reduction in primary panicles plant^{-1} (Table 3.2). The correlations between this component and the other two (seeds panicle^{-1} and 100-seed weight) were the lowest in both situations (Table 3.6), with three out of four of these correlations not different from zero.

When analyzing correlations between seed yield components and seed yield plant^{-1}, a better understanding is achieved when it is combined with path coefficient analysis. In this way, correlations can be partitioned into their component parts: the direct effect of that single component on seed yield, and the indirect effects through the correlation of that component with the others. Results of the path coefficient analyses for each defoliation treatment x year combination are shown in Table 3.7. The direct and indirect effects of each yield component with seed yield plant^{-1} are displayed in a concise tabular format proposed by Williams et al. (1990). Direct effects (path coefficients) are underlined in the main diagonal, while indirect effects are shown as off-diagonal elements. The sum of the direct and indirect effects give the correlation between the individual components and seed yield. In all situations, whether high yielding or low yielding, seeds panicle^{-1} was highly correlated with seed yield (always above 0.72). This was due to a high positive direct effect in all cases, and relatively low indirect effects through the other components. The same relationship was observed previously in a larger non-defoliated population, both phenotypically and genetically (discussed later in chapter 4). Defoliation did not alter this pattern, although the high direct effect of seeds panicle^{-1} was somewhat reduced in the lower-yield situations. With respect to primary panicles plant^{-1}, there was basically no relationship between this component and seed yield plant^{-1} in the high-yielding situations. Clearly, the direct effect of this component on seed yield plant^{-1} was important. However, it was always counterbalanced by the negative indirect effects through the other components, primarily seeds panicle^{-1}. This was due to the compensatory effects or negative correlations with the other components, which were discussed previously. 100-seed weight in the high-yielding situations also tended not

Table 3.7. Path-coefficient analysis of seed yield plant^{-1} and its components for every defoliation treatment x year combination. Direct effects (underlined) and indirect effects are shown for each seed yield component.

Seed yield component	Panicles plant^{-1}	Seeds panicle^{-1}	100-seed weight	r †	R^2‡
1991-No cuts					
Panicles plant^{-1}	0.65	-0.52	-0.14	-0.01	0.95
Seeds panicle^{-1}	-0.30	1.14	-0.07	0.78**	
100-seed weight	-0.19	-0.15	0.49	0.14	
1991-Two cuts					
Panicles plant^{-1}	0.29	-0.30	-0.02	-0.03	0.98
Seeds panicle^{-1}	-0.11	0.83	0.18	0.91**	
100-seed weight	-0.02	0.50	0.30	0.78**	
1991-Three cuts					
Panicles plant^{-1}	0.34	-0.01	0.13	0.46*	0.95
Seeds panicle^{-1}	-0.01	0.81	0.02	0.82**	
100-seed weight	0.16	0.05	0.28	0.48**	
1992-No cuts					
Panicles plant^{-1}	0.33	-0.24	-0.10	-0.02	0.95
Seeds panicle^{-1}	-0.08	0.96	0.05	0.93**	
100-seed weight	-0.17	0.24	0.20	0.28	
1992-Two cuts					
Panicles plant^{-1}	0.30	0.29	0.03	0.63**	0.97
Seeds panicle^{-1}	0.12	0.73	0.09	0.94**	
100-seed weight	0.08	0.55	0.12	0.75**	
1992-Three cuts					
Panicles plant^{-1}	0.38	0.02	0.14	0.53**	0.86
Seeds panicle^{-1}	0.01	0.53	0.18	0.72**	
100-seed weight	0.15	0.26	0.36	0.77**	

† Correlation of seed yield component with seed yield plant^{-1}. The addition of direct and indirect effects give this correlation.

‡ Coefficient of determination.

to correlate significantly with seed yield plant^{-1} due to compensatory mechanisms. This pattern was not as well defined as in panicles plant^{-1}. The correlations with seed yield were all positive (contrary to negative in the component panicles plant^{-1}) and plants cut twice in 1991 did not show this pattern, due to the positive indirect effect through seeds panicle^{-1}. This was caused by the positive correlation between seed weight and seeds panicle^{-1} (0.60 - Table 3.6). In the low-yielding situations, there was a positive correlation between panicles plant^{-1} and seed yield plant^{-1} (always above 0.46). Since compensatory effects were not observed in these cases, the positive direct effects were not counterbalanced by negative indirect effects. Indirect effects were low but positive, so they tended to increase the correlation with seed yield. 100-seed weight in the low-yield situations was highly correlated to seed yield plant^{-1} due to positive direct and indirect effects. For example, 100-seed weight of plants cut three times in 1992 (Table 3.7) had a modest direct effect of 0.36 on seed yield. However, the positive indirect effects through panicles plant^{-1} (0.15) and seeds panicle^{-1} (0.26), increased the correlation between 100-seed weight and seed yield plant^{-1} to a highly significant 0.77. A similar, albeit smaller, effect was observed in primary panicles plant^{-1}.

Summary

Two cuts per year in Gainesville, Florida, with the last cut around the beginning of August would appear to be a viable procedure for reducing the height and biomass of the plants, while maintaining relatively good seed production. Overall in 1991, plants cut twice yielded 28% more seed on average than uncut plants, due to a small increment in all its seed yield components, excluding secondary panicles tiller^{-1}. In 1992, there was a 44% reduction in seed yield of plants cut twice, primarily due to a

reduction in primary panicles plant^{-1}. Timing of fertilizer applications may have played an important role in this reduction. A fertilizer application after the second cut would have been more desirable. Germination of seed from plants cut twice was not reduced in 1991 and 1992. Neither was the persistence of these plants affected. The goal of achieving a reduction in the height and biomass of the plants, while maintaining adequate seed production and seed quality, seems feasible with the timing of these two cuts. Direct mechanized harvesting should be possible. However, cutting plants three times (last cut around mid-September) proved to be very detrimental for seed production. Elongating primary panicles were cut with this third harvest, therefore greatly reducing seed yield potential. Seed yield plant^{-1} dropped 77 and 98% in 1991 and 1992, respectively, compared to uncut plants. This was primarily due to reductions in primary panicles plant^{-1} and seeds panicle^{-1}. In addition, the probability of a frost affecting seed production is increased due to a delay in flowering. The survival of plants was also somewhat reduced with the third cut. Defoliating plants in September would not be recommended if seeds were to be harvested that fall.

Path-coefficient analyses indicated a change in the correlational structure among seed yield components due to defoliation. Negative correlations (compensatory effects) were observed among seed yield components in the high-yielding situations (uncut plants in both years and plants cut twice in 1991). However, in the low-yielding situations (plants cut twice in 1992 and three times in both years), correlations were either positive or not different from zero, showing that competition among components was negligible. Seeds panicle^{-1} was always highly correlated to seed yield plant^{-1}, due to high positive direct effects and relatively low indirect effects through the other components. In the high-yielding situations, primary panicles plant^{-1} and 100-seed

weight tended to not correlate significantly with seed yield plant^{-1}. Positive direct effects were counterbalanced by negative indirect effects. In the low-yielding situations, these components were positively correlated to seed yield, due to the lack of compensatory effects.

CHAPTER 4
CORRELATION AND PATH COEFFICIENT ANALYSES OF SEED YIELD COMPONENTS IN PEARL MILLET X ELEPHANTGRASS HYBRIDS

Introduction

An important goal in the pearl millet x elephantgrass [*Pennisetum glaucum* (L.) R.Br. x *P. purpureum* Schum.] breeding program at the University of Florida is to select populations with improved seed yield. Through increased seed yield, reliance on vegetative propagation, the major constraint limiting elephantgrass production on a large scale, could be reduced in many situations. Elephantgrass planting typically consists of placing whole stems horizontally in shallow furrows (Sollenberger et al., 1990). The high labor requirements and cost associated with establishment have limited the widespread use of this important forage and biomass species, especially in developed countries where labor is more expensive. Through hybridization with pearl millet and further breeding, a seeded high-quality elephantgrass interspecific hybrid ($2n$=$6x$=42) has been obtained (Schank and Diz, 1991; Diz and Schank, 1991). Seed yield plant^{-1} is very variable among genotypes, with coefficients of variation exceeding 100% (Diz and Schank, 1993).

Path-coefficient analysis (Wright, 1921) has been useful in determining selection criteria in a number of crops, including wheat (Fonseca and Patterson, 1968), maize (Ivanovic and Rosic, 1985), soybeans (Pandey and Torrie, 1973), sugarcane (Gravois et al., 1991; Kang et al., 1983), crested wheatgrass (Dewey and Lu, 1959), and tall

fescue (Sleper et al., 1977). In the case of seed yield, the importance of individual yield components, and their correlational structure with other components can be determined by path-coefficient analysis. Path-coefficient analysis measures the direct influence of one variable on another but also separates this correlation coefficient into components of direct and indirect effects (Li, 1975). Each correlation coefficient between a predictor variable and the response variable is partitioned into its component parts: the direct effect or path coefficient for the predictor variable (a standardized partial regression coefficient) and the indirect effects, which involve the product of a correlation coefficient between two predictor variables with the appropriate path coefficient in the path diagram. By determining the inter-relationships among seed yield components, a better understanding of both the direct and indirect effects of selecting for specific components can be attained.

The objectives of this research were 1) to evaluate the importance of the different seed yield components in pearl millet x elephantgrass hybrids; 2) to determine the direct and indirect effects of these components on seed yield through the use of path-coefficient analysis; and 3) to develop selection criteria for higher seed yield.

Materials and Methods

Data collected from a previous experiment were utilized for this analysis (Diz and Schank, 1993). Seven plants had been selected from a large heterogeneous pearl millet x elephantgrass hexaploid population. The selfed progeny of these 7 parental plants (S1 families) were used for the analysis. Their genealogy can be found in Diz and Schank (1993). A factorial experiment with a split-plot design and four replications was planted at the University of Florida, Gainesville, Florida (29° 48' N latitude) on 3

May 1990. The soil of the experimental site is classified as a Sparr fine sand; a sandy, siliceous, hyperthermic Grossarenic Paleudult. Main plots consisted of two seed sizes, large and small, while subplots consisted of the seven S_1 families. Each plot had six plants per row, spaced 0.9 m within the row and 2.7 m between rows. Plots were irrigated four times during May and June, due to a lower than normal rainfall. They received 190-48-95 kg ha^{-1} of $N\text{-}P_2O_5\text{-}K_2O$, split in two equal applications on 24 May and 7 July 1990. Seed yield components (tillers $plant^{-1}$, panicles $tiller^{-1}$, seeds $panicle^{-1}$, and 100-seed weight) were measured on each individual plant for a total of 336 plants. Tillers $plant^{-1}$ were determined on 24-28 Oct 1990. For panicles $tiller^{-1}$, four tillers $plant^{-1}$ were counted on 10 Dec 1990 and averaged for the analysis. Seeds $panicle^{-1}$ and 100-seed weight were obtained from one primary panicle $plant^{-1}$. Seed yield $plant^{-1}$ was calculated by multiplying tillers $plant^{-1}$, panicles $tiller^{-1}$ and seed yield $panicle^{-1}$. Other characteristics such as plant height, days to flowering, and panicle length were tested in the path models to determine whether the prediction of seed yield $plant^{-1}$ was improved. Since the coefficient of determination (R^2) was not improved, these characteristics were not included in the analyses.

Two path analyses were carried out according to the causal relationships portrayed in Fig. 4.1. One was constructed using phenotypic correlation coefficients, and the other using genetic correlation coefficients. The Statistical Analysis System (SAS, Institute Inc., 1985) was used to compute phenotypic correlation coefficients and standardized multiple regression analysis. Through the multiple regression analysis, standard partial regression coefficients (phenotypic path coefficients) were obtained. Analyses of variance and covariance were used to compute genetic correlations, using Harvey's Mixed Model Least-Squares program (Harvey, 1990). Genetic path

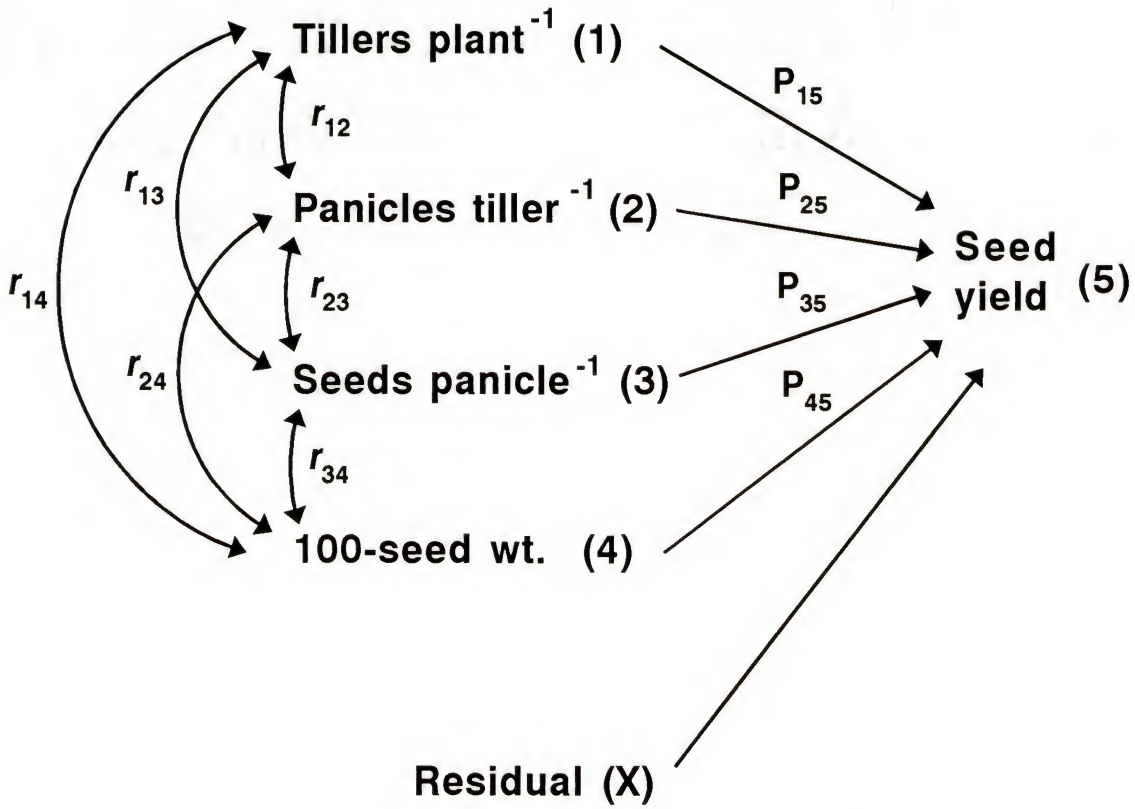

Fig. 4.1. Path diagram showing direct and indirect effects for four seed yield components in pearl millet x elephantgrass hybrids. Unidirectional arrows represent path coefficients (direct effects) while bidirectional arrows represent correlation coefficients between yield components.

coefficients were obtained by the simultaneous solution of the following equations:

$$P_{15} + r_{12}P_{25} + r_{13}P_{35} + r_{14}P_{45} = r_{15}$$

$$r_{12}P_{15} + P_{25} + r_{23}P_{35} + r_{24}P_{45} = r_{25}$$

$$r_{13}P_{15} + r_{23}P_{25} + P_{35} + r_{34}P_{45} = r_{35}$$

$$r_{14}P_{15} + r_{24}P_{25} + r_{34}P_{35} + P_{45} = r_{45}$$

The "P's" represent path coefficients and "*r*'s" denotes correlation coefficients. Indirect path coefficients were calculated as described by Li (1975) and Williams et al. (1990).

Results and Discussion

In Table 4.1, the means and standard deviations for the traits involved in the path analyses are shown for each S_1 family. Differences were found among families for tillers plant^{-1}, seeds panicle^{-1}, 100-seed weight, and seed yield plant^{-1} ($P<0.05$). There were differences among families for panicles tiller^{-1} at $P<0.10$. The coefficients of variation for each trait were high, especially for seed yield plant^{-1} (137%).

Phenotypic and genetic correlation coefficients for seed yield components and seed yield plant^{-1} are presented in Table 4.2. In several associations, these coefficients did not coincide, due to a relatively large environmental variance and covariance. In other cases, the influence of the environment on these relationships was minimal, therefore giving similar correlation coefficients (i.e., seeds panicle^{-1} with seed yield plant^{-1} and 100-seed weight). Due to these important differences found, path-coefficient analyses were carried out using phenotypic and genetic correlation coefficients in separate models. As shown in Table 4.2, important relationships were detected.

Table 4.1. S_1 family means ± standard deviations for the predictor and response variables used in the path-coefficient analyses.

S_1 family	Tillers plant^{-1}	Panicles tiller^{-1}	Seeds panicle^{-1}	100-seed weight	Seed yield plant^{-1}
	---------- No. ----------			mg	g
45B	22.1± 9.8	4.3±2.1	290±181	171±57	66±92
109A	19.2±12.3	4.0±2.9	110±104	159±53	29±45
127A	21.1±13.2	3.3±2.5	249±170	149±47	47±65
128B	22.6±11.2	4.2±1.9	302±190	205±56	83±93
131B	27.8±12.5	4.1±1.9	306±181	174±47	82±92
140B	26.2±13.8	4.0±2.5	185±129	172±51	66±97
144B	27.0±13.3	3.7±2.4	146±131	117±44	30±58
CV (%)†	53.4	57.9	67.9	30.1	137.2

†: Coefficient of variation

Table 4.2. Phenotypic and genetic correlation coefficients among seed yield components and seed yield plant^{-1}.†

Seed yield component	Panicles tiller^{-1}	Seeds panicle^{-1}	100-seed weight	Seed yield plant^{-1}
Tillers	0.29**	0.22**	0.13*	0.51**
plant^{-1}	-0.09	-0.28	-0.28	0.16
Panicles		0.23**	0.20**	0.51**
tiller^{-1}		-0.97*	0.35	-0.39
Seeds			0.56**	0.73**
panicle^{-1}			0.63*	0.80**
100-seed				0.59**
weight				1.08**

*,** Significant at the 0.05 and 0.01 probability level, respectively.

† Upper and lower correlation values are phenotypic and genetic, respectively.

Phenotypically, all seed yield components were positively and significantly associated with seed yield plant^{-1}. The component most highly correlated was seeds panicle^{-1} (r_p=0.73). Genetically, only two components were significantly correlated to seed yield plant^{-1}, seeds panicle^{-1} and 100-seed weight. Environmental variance of the other two components (tillers plant^{-1} and panicles tiller^{-1}) and the environmental covariance of these components with seed yield plant^{-1} were large, and hence resulted in non-significant correlations. Since a number of the plants evaluated were partially or completely sterile, the components tillers plant^{-1} and panicles tiller^{-1} were not as useful in predicting seed yield plant^{-1}. The component panicles tiller^{-1} had a genetically negative association with seed yield plant^{-1} (r_g=-0.39), although this was not significant. Among seed yield components, some important relationships could be observed. Both phenotypically and genetically, there was a strong positive association between seeds panicle^{-1} and 100-seed weight (r_p=0.55 and r_g=0.63). Because seed set was relatively low in these hybrids (means between 35-45%), an increase in seeds panicle^{-1} did not adversely affect the 100-seed weight. This usually does not hold true in crops where seed set is relatively high and the seed represents an important proportion of the total biomass of the plant. In these cases, the components seeds panicle^{-1} and 100-seed weight are usually negatively correlated because of competition among seeds for food reserves. This was not the case with these pearl millet x elephantgrass hybrids. To the contrary, plants with higher seeds panicle^{-1} tended to have larger seed. This relationship is very desirable because simultaneous improvement for both components could be accomplished by selecting for just one of these components. Another interesting relationship was panicles tiller^{-1} with seeds panicle^{-1}. Phenotypically, the relationship was positive but low (r_p=0.23). However, genetically, there was a high

negative correlation between these two components (r_g= -0.97). Genetically, those which produce high number of panicles tiller^{-1} would seem to be using a large proportion of energy in producing panicle structures rather than seed. This would explain why panicles tiller^{-1} was negatively associated with seed yield plant^{-1} (r_g= -0.39 ns). For higher seed yield and ease of harvesting, it would be more desirable to select for lower number of panicles tiller^{-1} and higher seeds panicle^{-1}. This could also be done simultaneously, due to their negative association.

Phenotypic and genetic path diagrams are illustrated in Figs. 4.2 and 4.3, respectively. Correlations among components and path coefficients are shown. These help understand the nature of the cause and effect of the seed yield system.

Results of the phenotypic and genetic path coefficient analyses are shown in Table 4.3. A concise tabular format proposed by Williams et al. (1990) is presented to indicate the correlational structures. Each table consists of a matrix with direct effects (path coefficients) in the main diagonal and indirect effects in both off diagonal portions, corresponding to their positions in the equations. The matrix is not symmetrical. For example, in the first phenotypic path in Table 4.3, one can observe that the correlation between tillers plant^{-1} and seed yield plant^{-1} is 0.51. This consists of four components; the direct effect (underlined) of tillers on seed yield plant^{-1} (0.30) and three indirect effects through its relationship with the other three yield components. Each one of these effects is partially contributing to the stated correlation in an additive manner. The addition of these four components gives 0.51.

All the phenotypic and genetic direct effects of seed yield components on seed yield plant^{-1} were positive. The greatest phenotypic and genetic direct effect was that of seeds panicle^{-1} (0.47 and 0.85, respectively). In the case of the phenotypic path

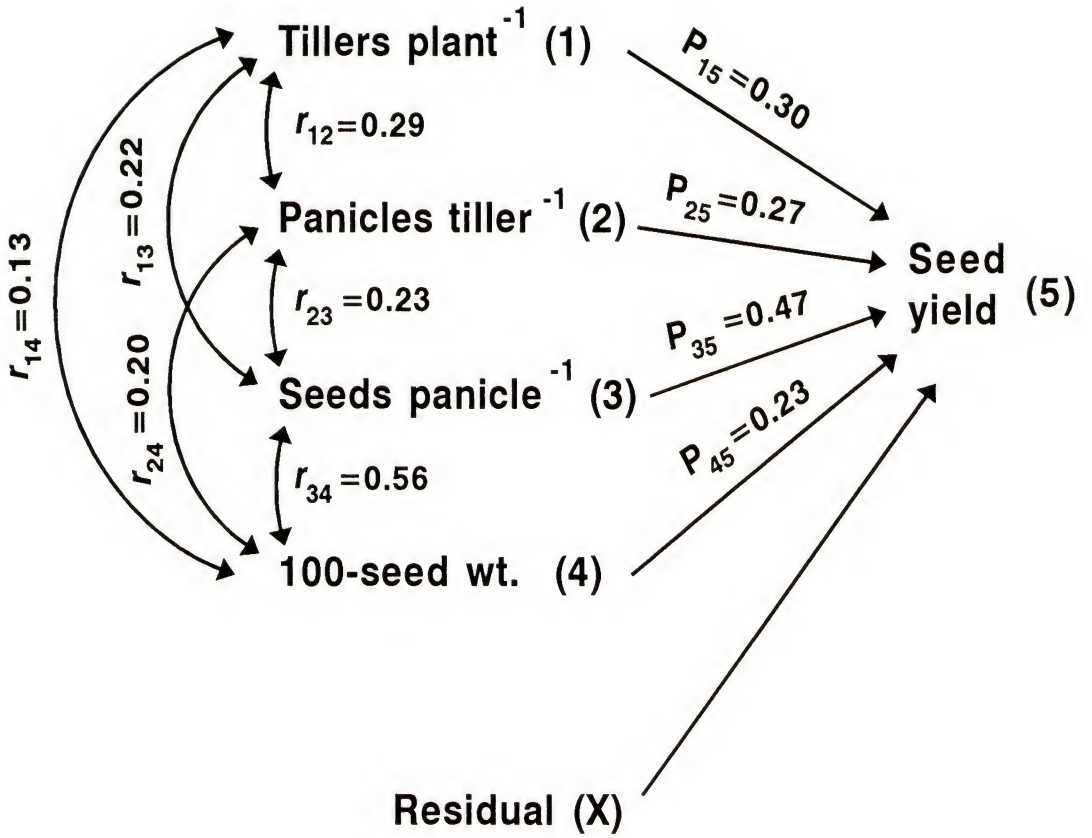

Fig. 4.2. Phenotypic path diagram showing the phenotypic correlation coefficients among seed yield components and direct path coefficients influencing seed yield plant^{-1}.

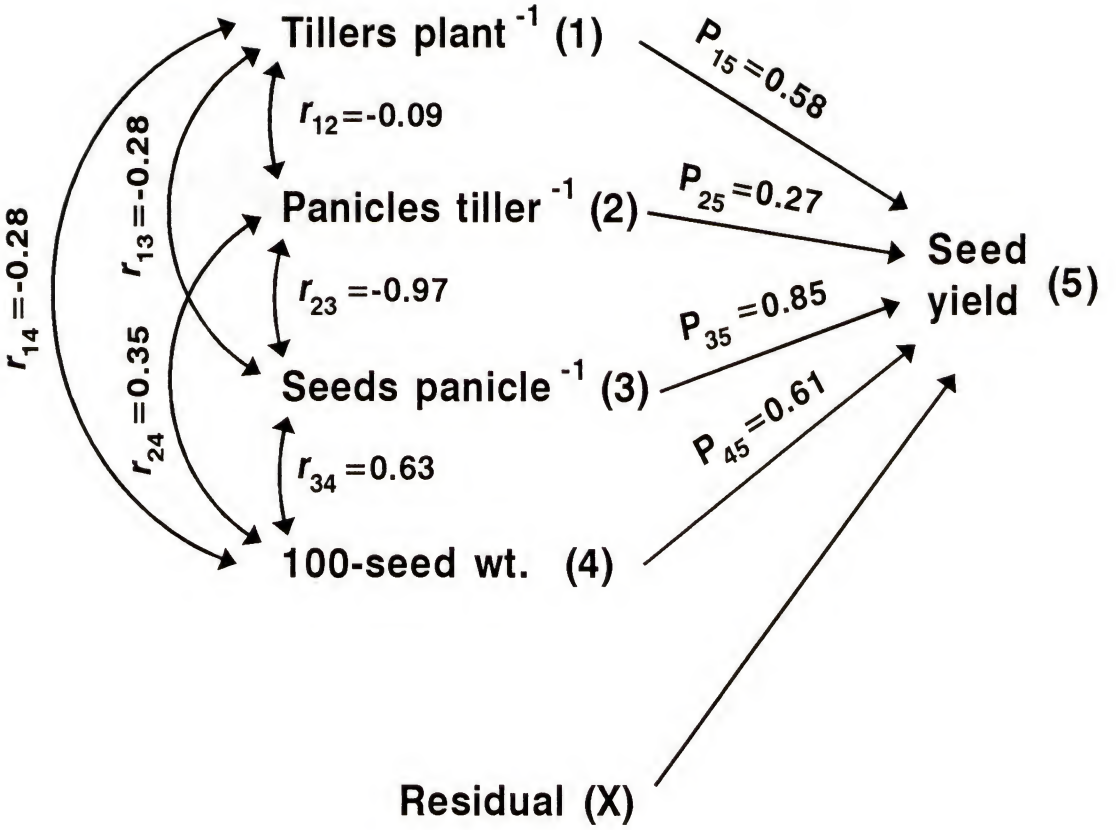

Fig. 4.3. Genetic path diagram showing the genetic correlation coefficients among seed yield components and direct path coefficients influencing seed yield plant^{-1}.

Table 4.3. Phenotypic and genetic path-coefficient analyses of seed yield and its components. Direct effects (underlined) and indirect effects on seed yield plant^{-1} are shown for each seed yield component.

Seed yield component	Tillers plant^{-1}	Panicles tiller^{-1}	Seeds panicle^{-1}	100-seed weight	r †
Phenotypic					
Tillers plant^{-1}	0.30	0.08	0.10	0.03	0.51
Panicles tiller^{-1}	0.09	0.27	0.11	0.05	0.51
Seeds panicle^{-1}	0.07	0.06	0.47	0.13	0.73
100-seed weight	0.04	0.05	0.26	0.23	0.59
Genetic					
Tillers plant^{-1}	0.58	-0.03	-0.24	-0.17	0.16
Panicles tiller^{-1}	-0.06	0.27	-0.82	0.21	-0.39
Seeds panicle^{-1}	-0.16	-0.27	0.85	0.38	0.80
100-seed weight	-0.16	0.10	0.53	0.61	1.08

† Correlation coefficient between components and seed yield plant^{-1}.

analysis, the direct effects were the ones that contributed mostly to the relationship between each seed yield component and seed yield plant^{-1}, except for the component 100-seed weight. In this case, the indirect effect through seeds panicle^{-1} was greater (0.26). For the other two components, tillers plant^{-1} and panicles tiller^{-1}, the indirect effects via seeds panicle^{-1} were also important (0.10 and 0.11, respectively). The indirect effect of 100-seed weight on seeds panicle^{-1} was also relatively important (0.13). However, phenotypically, direct effects had the greatest impact on seed yield.

A different correlational structure can be observed in the path analysis concerning genetic correlations. Direct effects were positive for every yield component, but indirect effects played a more important role and sometimes masked the direct effects. For example, panicles tiller^{-1} had a positive direct effect of 0.27, but this was masked by the larger indirect effect through seeds panicle^{-1} (-0.82). This result explains why panicles tiller^{-1} was negatively correlated (genetically) with seed yield plant^{-1}. The high negative correlation between panicles tiller^{-1} and seeds panicle^{-1} mentioned previously, was responsible for this negative indirect effect. If we consider tillers plant^{-1}, the relatively high and positive direct effect (0.58) was counterbalanced by three negative indirect effects, which made the genetic correlation between this component and seed yield plant^{-1} relatively low (0.16). With seeds panicle^{-1}, the indirect effects were essentially balanced, and so the direct effect was numerically similar to the correlation with seed yield plant^{-1} (0.85 vs 0.80). With 100-seed weight, the positive indirect effect through seeds panicle^{-1} exacerbated the direct effect, resulting in a correlation value slightly greater than 1.

Summary

The components seeds panicle^{-1} (primarily) and 100-seed weight exerted the greatest phenotypic influence both directly and indirectly on seed yield plant^{-1}. This was even more pronounced at the genetic level. Therefore, for increasing seed yield plant^{-1}, breeding efforts should emphasize these two components. Unfortunately, these two components are the most difficult to evaluate and measure in a large breeding nursery, when compared to tillers plant^{-1} or panicles tiller^{-1}. These two latter components had positive direct effects on seed yield plant^{-1}, but relatively small indirect effects through other components. The path-coefficient analysis concerning genetic correlations is more relevant for breeders, because the genetic causes of correlation have been separated from the environmental causes of correlation. When heritability values of characteristics are low, then the phenotypic correlation is determined primarily by the environmental correlation (Falconer, 1989). For this reason, phenotypic correlations may sometimes be misleading from a breeding point of view. For example, the components panicles tiller^{-1} and seeds panicle^{-1} were positively associated phenotypically; but once the environmental causes of correlation were eliminated, the genetic association between these two components was highly negative. So simultaneous selection for increasing these two components would not be possible, due to compensatory mechanisms. This was not the picture portrayed by the phenotypic correlation, where the correlation was small but positive. Another interesting association was that between seeds panicle^{-1} and 100-seed weight. These were positively associated both phenotypically and genetically, so simultaneous selection for both components would be desirable and effective. This is not a common association among economically important crops.

CHAPTER 5
HERITABILITIES, GENETIC PARAMETERS, AND RESPONSE TO SELECTION IN PEARL MILLET X ELEPHANTGRASS HYBRIDS

Introduction

Development of high-quality, seed-propagated warm season grasses is very important for beef and dairy cattle in the tropics and subtropics. Pearl millet x elephantgrass amphiploid hybrids ($2n=6x=42$) have many desirable attributes which may make this grass a suitable forage (Diz and Schank, 1991; Muldoon and Pearson, 1979; Schank and Diz, 1991). The pearl millet x elephantgrass F_1 hybrids are sterile triploids, but fertility can be restored by chromosome doubling (Hanna, 1981). These amphiploids (hexaploids) behave meiotically like typical allohexaploids, possessing a high degree of regular meiosis and a wide range of pollen and seed fertility. They usually form 21 bivalents during meiosis (Jauhar, 1981; Jauhar and Singh, 1969), with multivalent associations rarely observed.

Further breeding of these grasses will be required if hexaploid varieties are to be developed. Plants with low number of tillers, low leaf to stem ratio, extremely tall or short, very low seed production, and poor persistence are not uncommon in hybrid breeding nurseries. Large genetic variability was found in these and other important characteristics (Diz and Schank, 1993). Heritability estimates and genetic correlations are very useful in improving the efficiency of a breeding program through the development of appropriate selection strategies. To date, heritability estimates and

other genetic parameters have not been published for these hybrids. Several studies have been published for pearl millet, a major cereal and forage crop which has been bred intensively. Due to the importance of this crop in India, numerous publications have resulted from research in that country. Rachie and Majmudar (1980) have summarized heritability and correlation values reported for several pearl millet characteristics. High heritabilities have been estimated for plant height, maturity date, head length, and grain size, whereas leaf size and number of tillers have yielded more moderate estimates. Heritability estimates have varied considerably for characters such as forage yield or grain yield. Correlations of grain yield or heading date with plant height have been inconsistent. Gupta and Athwal (1966) found negative or positive correlations depending on the germplasm source. They also found negative correlations between plant height and number of tillers, regardless of germplasm source. In more recent studies, Rattunde et al. (1989) obtained relatively high narrow-sense heritability estimates for 19 traits in S_0-S_1 progeny pairs, while Sastry et al. (1987) obtained relatively low broad-sense heritability estimates from S_1 progenies. Grain yield and seed-related traits were among the lowest estimates in both cases, with heritabilities of 0.29 and 0.27 for grain yield and panicle yield, respectively (Rattunde et al., 1989), while heritability for panicle weight was not different from zero in Sastry et al. (1987). Because our *Pennisetum* hybrids are amphiploids and two thirds of their genetic constitution is derived from elephantgrass, heritabilities and other genetic parameters may differ considerably from those of pearl millet.

The objectives of this study were i) to estimate heritabilities on a single-plant basis for number of tillers, plant height, leaf length, leaf width, days to flowering, panicle length, seed set, seed yield panicle^{-1}, seeds panicle^{-1}, seed yield plant^{-1}, and 100-seed

weight; ii) to calculate genetic, phenotypic, and environmental correlations among these traits, iii) estimate the response to selection for all traits, and iv) calculate predicted correlated responses for specific pairs of traits where indirect selection would be more efficient than direct selection.

Materials and Methods

The experiment was conducted at the Dairy Research Unit of the University of Florida, Gainesville (29° 48' N latitude). The soil of the experimental site is classified as a Sparr fine sand; a sandy, siliceous, hyperthermic Grossarenic Paleudult. Data used for the estimation of genetic parameters were collected in 1990 and 1992 from a factorial experiment involving seven S_1 families. Data were not collected in 1991 because plans of using this experiment for a quantitative genetics study arose at the end of 1991, too late for data collection that year. The genealogy of the families included in this experiment has been previously described (Diz and Schank, 1991 and 1993). The experimental design was a split-plot with four replications, planted on 3 May 1990. Main plots consisted of two seed sizes, large and small, while subplots consisted of the seven S_1 families. Each plot contained six plants in a row, spaced 0.9 m within the row and 2.7 m between rows. The experiment was irrigated four times during May and June, 1990, during a low rainfall period. Plots received 190-48-95 and 166-42-83 kg ha^{-1} of $N\text{-}P_2O_5\text{-}K_2O$ in 1990 and 1992, respectively. Characteristics measured on each individual plant in both years included number of tillers, plant height, leaf length, leaf width, days to flowering, panicle length, seed set, seed yield $panicle^{-1}$, seeds $panicle^{-1}$, seed yield $plant^{-1}$, and 100-seed weight. Details on their measurement have been described previously (Diz and Schank, 1993). A total of 336

plants were measured in 1990 but due to lack of plant persistence, only 202 plants were measured in 1992. This was detrimental for the estimation of genetic parameters because of the reduced number of plants evaluated and the effect of selection (natural selection for persistence) on genetic and phenotypic variance components. However, selection in our breeding program sometimes involves selecting plants from older stands, primarily to improve persistence. Estimates in 1992 can therefore provide useful information on how these genetic parameters vary in older stands.

Analyses of variance were performed for every characteristic using the general linear model procedure of the Statistical Analysis System (SAS Institute Inc., 1985). Due to significant year effects for most characteristics and that 1992 data was affected by persistence, years were analyzed separately. Heritability estimates and genetic, phenotypic, and environmental correlations were calculated for each year. Harvey's Least-squares program (Harvey, 1990) was used for these estimates. For the analyses, S_1 families (F) were considered random, while seed-size (S) was considered fixed. When the FxS interaction was significant, this additional source of variation was taken into account for the estimates. Data was analyzed using model 6 of Harvey's program, the model for the randomized block split-plot design with one set of cross-classified random effects interacting with one set of cross-classified fixed effects. Model 2 was used when the FxS interaction was not significant, the model for one set of cross-classified random effects not interacting with the set of fixed effects. In this case the FxS interaction was included in the error term due to its lack of significance. Table 5.1 shows the degrees of freedom, expectations of mean squares, and k-coefficients for each characteristic in the individual year analyses of variance. Variance components were calculated from these analyses. Some traits had larger

Table 5.1. Expected mean squares (EMS), degrees of freedom (df), and coefficients (k_n) for individual year analyses of variance for the *Pennisetum* hybrid families.

When F x S† interaction not significant:

Source	df	EMS
Family (F)	6	$\sigma_e^2 + k_2\sigma_F^2$
Size (S)	1	$\sigma_e^2 + k\theta_S^2$
Error	df_e	σ_e^2

When F x S interaction significant:

Source	df	EMS
Family (F)	6	$\sigma_e^2 + k_3\sigma_F^2$
Size (S)	1	$\sigma_e^2 + k\sigma_{FS}^2 + k\theta_S^2$
FxS	6	$\sigma_e^2 + k_1\sigma_{FS}^2$
Plant (FS)	$df_{P(FS)}$	σ_e^2

Degrees of freedom and Coefficients:

	1990		1992				
Characteristic	df_e	k_2	df_e	$df_{P(FS)}$	k_1	k_2	k_3
Tiller no.	328	48.000	194			28.584	
Plant height	328	48.000	194			28.584	
Leaf length	328	48.000	194			28.584	
Leaf width	328	48.000	194			28.584	
Days to flowering ‡	328	48.000		188	13.764		28.584
Panicle Length	320	46.852	194			28.584	
Seed set	320	46.852	194			28.584	
Seed yield panicle^{-1} ‡	320	46.852		188	13.764		28.584
Seeds panicle^{-1} ‡	320	46.852		165	12.053		25.214
Seed yield plant^{-1}	320	46.852	194			28.584	
100-seed weight ‡	279	40.858		142	10.357		21.778

† F x S: Family x seed size

‡ Significant family x seed size interaction in 1992 ($P<0.05$).

degrees of freedom (df) for the error term because more plants were measured for that trait. 100-seed weight had the lowest df in both years because some plants produced very few seed or none at all. Covariance components were calculated from the analyses of covariance, with the expected mean products following the same structure as in the analysis of variance. The covariance of S_1 sibs is less simple than those of other relationships such as half-sibs. Using Cotterman k-coefficients (Crow and Kimura, 1970), the coefficients for the additive, dominance, and epistatic variance components were calculated. The covariance of S_1 sibs was calculated as:

$$COV_{S1} = \frac{2}{3}\sigma^2_A + \frac{1}{2}\sigma^2_D + \frac{4}{9}\sigma^2_{AA} + \frac{1}{4}\sigma^2_{DD} + \frac{1}{3}\sigma^2_{AD}$$

when only two-factor interactions were included. The variance components σ^2_A and σ^2_D denote additive and dominance genetic variance, respectively. The components σ^2_{AA}, σ^2_{DD}, and σ^2_{AD} indicate the two-factor epistatic variance components. By multiplying COV_{S1} by 1.5 in the heritability estimates, the total σ^2_A was accounted for, together with portions of dominance and epistatic variance components. Therefore, these are neither narrow-sense nor broad-sense heritability estimates, but somewhat intermediate. They are narrow-sense only if we assume that the dominance and epistatic variance components are equal to zero. When the FxS interaction was significant, heritabilities were estimated as:

$$h^2 = \frac{1.5\sigma^2_F}{\sigma^2_F + \sigma^2_{FS} + \sigma^2_e}$$

and according to the following when the FxS interaction was not significant:

$$h^2 = \frac{1.5\sigma^2_F}{\sigma^2_F + \sigma^2_e}$$

where σ^2_F is the family variance component (which is an estimate for COV_{S1}), σ^2_{FS} the FxS variance component, and σ^2_e the error variance component.

Genetic, phenotypic, and environmental correlations were calculated as described by Harvey (1990). Predicted response to selection was calculated for all characteristics through the following equation: $R = i\, h^2\, \sigma_p$; where R is the predicted response to selection; *i* the intensity of selection; h^2 the heritability, and σ_p the phenotypic standard deviation. R values were calculated for an *i* value of 1.755, which represents selecting the best 10% of a breeders large population (Appendix Table A in Falconer, 1989), assuming a normal distribution of values in the population. Correlated responses, or the expected response of a character Y when selecting for another character x, were calculated for specific pairs of characters as: $CR_y = i_x\, h_x\, h_y\, r_g\, \sigma_{py}$; where CR_y is the correlated response of character y; *i* the intensity of selection on character x; h_x and h_y the square root of the heritabilities for characters x and y; r_g the genetic correlation between characters x and y; and σ_{py} the phenotypic standard deviation for character y.

Results

S_1 family means for the 11 traits evaluated in 1990 and 1992 are shown in Table 5.2. Overall family means for the vegetative traits were greater in 1992 than 1990, but means of reproductive traits were lower in 1992. Results for the combined-year and single-year analyses of variance are shown in Table 5.3. Family differences were found for all traits in the combined-year analyses and the 1990 analyses. However, differences were not significant for leaf length and the seed-related traits (except 100-seed weight) among families in 1992. Presumably, plant loss was a primary factor in this result. In the combined-year analyses, year differences were apparent in all traits

Table 5.2. S_1 family means in 1990 and 1992 for the characteristics measured in the pearl millet x elephantgrass hexaploid hybrids.

Characteristic	Unit	S_1 family							LSD	Overall
		45B	109A	127A	128B	131B	140B	144B	(0.05)	mean
1990										
Tiller no.	no. plant^{-1}	22.1	19.2	21.1	22.6	27.8	26.2	27.0	5.0	23.7
Plant height	m	3.22	2.70	3.07	2.93	2.92	2.90	2.65	0.27	2.91
Leaf length	cm	83.9	77.8	82.7	78.6	79.7	77.6	73.2	5.9	79.1
Leaf width	cm	4.18	3.69	4.22	4.19	3.65	4.01	3.71	0.33	3.95
Days to flowering	days	166	174	176	160	165	169	170	5.6	169
Panicle length	cm	22.7	19.8	21.8	21.0	21.5	20.2	19.0	1.8	20.9
Seed set	%	47.4	22.4	40.7	44.4	46.4	36.3	20.7	9.6	36.9
Seed yield panicle^{-1}	g panicle^{-1}	0.54	0.20	0.41	0.64	0.59	0.35	0.20	0.15	0.42
Seeds panicle^{-1}	no.	290	110	249	302	306	185	147	63	227
Seed yield plant^{-1}	g	12.8	5.2	10.3	16.0	17.4	11.7	6.2	5.2	11.4
100-seed weight	mg	171	159	149	205	174	172	117	22	164
1992										
Tiller no.	no. plant^{-1}	27.4	23.7	30.2	28.7	39.5	31.2	32.5	8.2	30.5
Plant height	m	3.38	3.24	3.47	3.10	3.22	3.23	2.89	0.36	3.22
Leaf length	cm	98.5	100.5	98.2	94.9	99.5	95.1	92.0	NS†	97.0
Leaf width	cm	4.43	4.38	4.72	4.42	4.00	4.32	3.93	0.38	4.31
Days to flowering	days	173	173	175	163	172	171	176	5.5	172
Panicle length	cm	21.2	21.5	21.4	22.5	19.5	20.9	17.9	2.7	20.7
Seed set	%	28.8	14.5	26.8	22.0	26.2	17.4	16.5	NS	21.7
Seed yield panicle^{-1}	g panicle^{-1}	0.31	0.18	0.23	0.31	0.28	0.14	0.11	0.15	0.22
Seeds panicle^{-1}	no.	174	110	147	176	152	86	115	NS	137
Seed yield plant^{-1}	g	9.1	4.0	7.8	9.3	10.6	4.8	3.5	NS	7.0
100-seed weight	mg	162	172	144	187	172	159	125	27	160

† NS: Not significant.

Table 5.3. Significance of main effects and relevant interactions in the combined year and individual year analyses for the characteristics studied in the hybrid *Pennisetums*.

	Combined years (1990,1992)				1990 Analysis			1992 Analysis		
Characteristic	Family	Size†	Year	FxS‡	Family	Size†	FxS‡	Family	Size†	FxS‡
Tiller no.	**		**		**			**		
Plant height	**	**	**		**	**		*		
Leaf length	**		**		*	*				
Leaf width	**	*	**		**	*		**		
Days to flowering	**		**	*	**	*		**		**
Panicle length	**				**	**		*		
Seed set	**		**		**					
Seed yield panicle^{-1}	**		**	*	**				*	*
Seeds panicle^{-1}	**	*	**	**	**	*			*	*
Seed yield plant^{-1}	**		**		**					
100-seed weight	**				**			**		*

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Seed size
‡ Family x seed size interaction.

except panicle length and 100-seed weight. Environmental differences and natural selection for persistence during 2 years were probably responsible for the year differences. The family x year interaction was not significant for any trait, so the additional source of variation due to this interaction component was negligible. The family x seed-size (FxS) interaction was not significant for any trait in 1990, but was significant for days to flowering, seed yield panicle^{-1}, seeds panicle^{-1}, and 100-seed weight in 1992. Single-plant heritability estimates differed among the 11 traits and were very low to moderate (Table 5.4). Within family variation was usually large for all traits, thus reducing heritabilities. Among the vegetative characteristics, leaf width had the highest heritability. Heritabilities for reproductive characteristics were moderate in 1990, with highest heritabilities for 100-seed weight (0.30) and seeds panicle^{-1} (0.29). However, in the 1992 population, heritabilities were very low for reproductive characteristics except for days to flowering and 100-seed weight. The reason was that family differences in 1992 were not significant for seed set, seed yield panicle^{-1}, seeds panicle^{-1}, and seed yield plant^{-1}. The heritability estimates for these characteristics in 1992 were less reliable because the lack of genetic variation among families reduced the estimates to negligible values. The same was true for leaf length in 1992. These values were included in Table 5.4 to show this effect, although it is not appropriate to calculate heritabilities when family differences are not significant.

Genetic (r_g), phenotypic (r_p), and environmental (r_e) correlations among characteristics in 1990 and 1992 are shown in Tables 5.5 and 5.6, respectively. In some cases, the r_g and r_p differed in magnitude and sign. In others, the two had the same sign and were not very different in magnitude. A large difference, especially a change in sign, indicates that genetic and environmental sources of variation affected

Table 5.4. Heritability estimates (± SE) from variance component analysis of selfed (S_1) families in 1990 and 1992, for the agronomic characteristics evaluated.

Characteristic	Heritability estimates (h^2)†		
	1990	1992	Mean
Tiller no.	0.07 ± 0.06	0.10 ± 0.08	0.09
Plant height	0.09 ± 0.07	0.06 ± 0.06	0.07
Leaf length	0.05 ± 0.05	0.02 ± 0.04	0.04
Leaf width	0.11 ± 0.07	0.16 ± 0.11	0.13
Days to flowering	0.23 ± 0.13	0.15 ± 0.11	0.19
Panicle length	0.09 ± 0.07	0.08 ± 0.07	0.09
Seed set	0.24 ± 0.13	0.04 ± 0.05	0.14
Seed yield panicle^{-1}	0.27 ± 0.14	0.07 ± 0.06	0.17
Seeds panicle^{-1}	0.29 ± 0.15	0.06 ± 0.07	0.18
Seed yield plant^{-1}	0.14 ± 0.09	0.05 ± 0.06	0.10
100-seed weight	0.30 ± 0.15	0.17 ± 0.12	0.24

† Individual plant heritabilities estimated as:

$$h^2 = \frac{1.5\,\sigma_F^2}{\sigma_F^2 + \sigma_e^2}$$ (when family x seed size interaction not significant)

$$h^2 = \frac{1.5\,\sigma_F^2}{\sigma_F^2 + \sigma_{FS}^2 + \sigma_e^2}$$ (when family x seed size interaction significant)

Table 5.5. Genetic (r_g), phenotypic (r_p), and environmental (r_e) correlations among the characteristics evaluated in the pearl millet x elephantgrass hexaploid hybrid families in 1990.

Characteristic	r	Plant height	Leaf length	Leaf width	Days to flowering	Panicle length	Seed set	Seed yld panicle^{-1}	Seeds panicle^{-1}	Seed yld plant^{-1}	100-seed weight
Tiller no.	r_g	-0.47±0.44	-0.83±0.31	-0.57±0.42	-0.46±0.44	-0.52±0.41	-0.04±0.50	0.00±0.50	0.07±0.49	0.24±0.49	-0.31±0.48
	r_p	0.46	0.30	0.09	-0.38	0.36	0.21	0.24	0.28	0.55	0.12
	r_e	0.54	0.37	0.15	-0.37	0.45	0.26	0.29	0.33	0.59	0.21
Plant height	r_g		0.99±0.07	0.80±0.21	-0.02±0.50	1.03±0.05	0.98±0.09	0.74±0.24	0.81±0.19	0.60±0.34	0.36±0.46
	r_p		0.80	0.61	-0.54	0.72	0.47	0.54	0.59	0.55	0.29
	r_e		0.79	0.58	-0.64	0.69	0.40	0.52	0.58	0.55	0.30
Leaf length	r_g			0.66±0.34	0.28±0.52	1.08±0.09	0.92±0.19	0.64±0.34	0.69±0.31	0.47±0.44	0.33±0.59
	r_p			0.56	-0.33	0.63	0.37	0.43	0.47	0.41	0.21
	r_e			0.56	-0.43	0.60	0.31	0.42	0.47	0.41	0.22
Leaf width	r_g				-0.04±0.49	0.67±0.32	0.64±0.31	0.53±0.36	0.53±0.35	0.31±0.46	0.29±0.45
	r_p				-0.24	0.42	0.34	0.39	0.41	0.30	0.23
	r_e				-0.28	0.39	0.29	0.37	0.40	0.30	0.22
Days to flowering	r_g					-0.06±0.50	-0.50±0.37	-0.73±0.26	-0.62±0.31	-0.80±0.26	-0.74±0.25
	r_p					-0.50	-0.34	-0.39	-0.39	-0.39	-0.39
	r_e					-0.59	-0.29	-0.28	-0.31	-0.30	-0.24
Panicle length	r_g						1.02±0.08	0.84±0.18	0.90±0.13	0.67±0.30	0.38±0.52
	r_p						0.44	0.54	0.56	0.51	0.30
	r_e						0.34	0.48	0.51	0.49	0.31
Seed set	r_g							0.96±0.05	0.97±0.04	0.94±0.08	0.73±0.23
	r_p							0.83	0.84	0.71	0.65
	r_e							0.79	0.80	0.66	0.64

(Continued)

Table 5.5. (Continued).

Characteristic	r	Plant height	Leaf length	Leaf width	Days to flowering	Panicle length	Seed set	Seed yld panicle^{-1}	Seeds panicle^{-1}	Seed yld plant^{-1}	100-seed weight
Seed yield panicle^{-1}	r_g								0.97±0.02	0.97±0.04	0.84±0.14
	r_p								0.94	0.88	0.76
	r_e								0.92	0.89	0.74
Seeds panicle^{-1}	r_g									0.94±0.07	0.64±0.27
	r_p									0.82	0.55
	r_e									0.81	0.53
Seed yield plant^{-1}	r_g										0.84±0.17
	r_p										0.63
	r_e										0.6

Table 5.6. Genetic (r_g), phenotypic (r_p), and environmental (r_e) correlations among the characteristics evaluated in the pearl millet x elephantgrass hexaploid hybrid families in 1992.

Characteristic	r	Plant height	Leaf length	Leaf width	Days to flowering	Panicle length	Seed set	Seed yld panicle^{-1}	Seeds panicle^{-1}	Seed yld plant^{-1}	100-seed weight
Tiller no.	r_g	-0.65±0.45	-0.28±0.87	-0.89±0.32	0.28±0.54	-1.02±0.28	0.31±0.70	-0.05±0.64	-0.02±0.64	0.36±0.60	0.08±0.55
	r_p	0.41	0.22	-0.09	-0.24	0.14	0.09	0.04	0.04	0.36	-0.10
	r_e	0.50	0.25	0.02	-0.31	0.26	0.08	0.05	0.05	0.36	-0.12
Plant height	r_g		1.02±0.48	0.89±0.25	0.56±0.63	0.50±0.51	1.07±0.45	0.62±0.55	-0.42±1.21	0.46±0.64	-
	r_p		0.59	0.54	-0.58	0.69	0.28	0.31	0.30	0.39	0.10
	r_e		0.58	0.51	-0.72	0.71	0.24	0.30	0.31	0.39	-
Leaf length	r_g			0.38±0.78	0.53±0.98	0.27±0.87	1.09±0.86	1.13±0.79	-†	1.01±0.80	-
	r_p			0.34	-0.39	0.49	0.24	0.23	0.19	0.24	0.05
	r_e			0.35	-0.46	0.51	0.21	0.20	-	0.22	-
Leaf width	r_g				-0.08±0.53	1.01±0.15	0.40±0.61	0.34±0.54	0.11±0.68	0.05±0.65	-0.24±0.54
	r_p				-0.30	0.49	0.26	0.31	0.29	0.29	0.24
	r_e				-0.34	0.43	0.25	0.31	0.33	0.32	0.33
Days to flowering	r_g					-0.64±0.54	0.07±0.68	-0.69±0.49	-0.18±0.67	-0.55±0.59	-0.39±0.52
	r_p					-0.56	-0.16	-0.21	-0.18	-0.23	-0.21
	r_e					-0.54	-0.21	-0.16	-0.19	-0.21	-0.17
Panicle length	r_g						0.24±0.72	0.68±0.43	-	0.35±0.64	0.29±0.75
	r_p						0.29	0.41	0.41	0.35	0.34
	r_e						0.30	0.39	-	0.35	0.36
Seed set	r_g							0.79±0.30	1.03±0.16	0.99±0.17	-
	r_p							0.84	0.87	0.75	0.58
	r_e							0.84	0.87	0.74	-

(Continued)

Table 5.6. (Continued).

Characteristic	r	Plant height	Leaf length	Leaf width	Days to flowering	Panicle length	Seed set	Seed yld panicle^{-1}	Seeds panicle^{-1}	Seed yld plant^{-1}	100-seed weight
Seed yield panicle^{-1}	r_g								0.94±0.09	0.99±0.09	0.88±0.17
	r_p								0.96	0.86	0.76
	r_e								0.97	0.85	0.74
Seeds panicle^{-1}	r_g									0.94±0.18	0.69±0.38
	r_p									0.84	0.65
	r_e									0.84	0.66
Seed yield plant^{-1}	r_g										0.97±0.25
	r_p										0.57
	r_e										0.53

† -: Genetic or environmental correlation could not be calculated due to a negative family variance component for one of the characteristics.

the traits through different physiological mechanisms (Falconer, 1989). Some correlations were consistent over years, despite the population size reduction in 1992. Among vegetative traits, number of tillers was negatively associated genetically with plant height and leaf characters, but positively associated phenotypically and environment-ally with plant height and leaf length. In general, days to flowering was negatively associated with vegetative and reproductive traits. Reproductive traits were highly correlated among themselves genetically, phenotypically, and environmentally. Plant height and leaf length were also consistently correlated with reproductive characters.

Phenotypic standard deviations and predicted responses to selection, assuming a 10% of the population selected (i = 1.755), are shown in Table 5.7. Large phenotypic variation was encountered in both years for all traits. CV's were highest for number of tillers and seed-related traits. Except for number of tillers, plant height, and panicle length, variation was larger in 1990 than 1992. The loss of plants in 1992 was partially responsible for this reduction. Additionally, a common scale effect, namely a decrease in variances when the mean decreases, probably affected reproductive traits. Predicted response was relatively low for vegetative characters, days to flowering, and panicle length. In the vegetative characteristics, number of tillers had the highest predicted response in both years due to its larger phenotypic variation. In spite of the moderate to low heritabilities for seed characters in 1990, predicted responses to selection were high due to the large phenotypic variations. Highest predicted responses were for seed yield panicle^{-1} and seeds panicle^{-1}, with expected mean increases of 43 and 37% after one cycle of selection, respectively. Predicted

Table 5.7. Phenotypic standard deviations (σ_p) and predicted response to selection (R)† for the characters evaluated in the *Pennisetum* hybrids.

Character	unit	1990 σ_p	1992 σ_p	R (1990)		R (1992)	
				units	%‡	units	%‡
Tiller no.	no. plant^{-1}	12.67	15.77	1.49	6.3	2.69	8.7
Plant height	m	0.695	0.703	0.106	3.6	0.065	2.0
Leaf length	cm	15.05	13.72	1.34	1.7	0.48	0.5
Leaf width	cm	0.86	0.76	0.15	3.8	0.20	4.6
Days to flowering	days	14.64	11.86	5.55	3.3	2.98	1.7
Panicle length	cm	4.54	5.30	0.67	3.2	0.73	3.5
Seed set	%	26.31	21.60	10.44	28.2	1.50	6.7
Seed yield panicle^{-1}	g panicle^{-1}	0.407	0.302	0.179	42.6	0.033	14.2
Seeds panicle^{-1}	no.	173.4	132.7	83.2	36.6	13.2	9.3
Seed yield plant^{-1}	g	13.48	10.79	3.19	28.0	0.95	12.8
100-seed weight	mg	57	49	28	16.9	14	8.8

† Predicted response to selection calculated as: $R = i\, h^2\, \sigma_p$, assuming an intensity of selection (*i*) of 1.755 (10% of the population selected).

‡ R(%) calculated as $\frac{R}{Mean} \times 100$

responses to selection for seed characters in 1992 were lower, primarily due to the lack of significance among families.

The correlated response on character y when selecting for character x can be more effective than the response to direct selection on y, if the following is true:

$$h_x \times r_g > h_y$$

where h_x and h_y are the square root of the heritabilities for characters x and y, and r_g is the genetic correlation between these characters. In 1990, predicted correlated responses (CR) which were greater than the predicted direct responses (R) to selection were found for a few pairs of characters. For improving seed yield plant^{-1}, it was more efficient to select indirectly through days to flowering (CR = 36.1%), seed set (CR = 36.2%), seed yield panicle^{-1} (CR = 39.3%), seeds panicle^{-1} (CR = 39.7%), and 100-seed weight (CR = 36.1%) than to select directly for seed yield plant^{-1} (R = 28%). For increasing vegetative characters such as plant height or leaf length, the predicted correlated responses through seed characters such as seed set, seed yield panicle^{-1}, and seeds panicle^{-1} were greater than the predicted responses when selecting directly for these traits. However, it would be inappropriate for a breeder only interested in plant height or leaf length to pursue this type of correlated response because of the tedious work involved in measuring the seed-related traits. Correlated responses were not calculated for 1992 because of the lack of significance among families for the seed related traits.

Discussion

In this study, year differences were due not only to environmental differences but also to a reduction in the population number through natural selection for persistence.

In general, lack of survivability reduced the variance components and thus confounded the year effect. For this reason, 1992 estimates are probably less reliable. However, they do indicate changes in the estimates that occurred naturally in this population. Family differences, critical to heritability estimates, became non-significant for leaf length and most seed-related traits. Hence, heritabilities were lower in 1992 for almost all traits. When compared to estimates reported for pearl millet, heritabilities calculated in this study were low, although some authors have reported similar estimates in pearl millet (Rachie and Majmudar, 1980; Sastry et al., 1987). In this population, improvement of certain characters through phenotypic selection would be slow unless improved selection procedures were utilized. Improvement of seed-related characters and number of tillers should be faster because of higher heritabilities and greater phenotypic variation in the population. Effectiveness of phenotypic selection would be maximized by any technique that would increase heritability on a single-plant basis. For example, recurrent restricted phenotypic selection (Burton, 1974), where environmentally induced plant-to-plant differences are limited to those occurring within a small area of the nursery, would probably increase the response to selection. Genotypic selection would be more efficient for traits with very low heritabilities, but the time needed per cycle of selection would increase.

Effects on other traits when selecting for a specific trait can be understood through genetic correlations. Selecting for higher number of tillers should reduce plant height, both desirable from a forage point of view. This same association was observed in pearl millet by Gupta and Athwal (1966), regardless of the germplasm source evaluated. Phenotypically, the opposite seemed true because the phenotypic correlation between number of tillers and plant height was positive. Selecting for

earlier flowering should increase vegetative characters (not desirable for plant height) and improve seed production, which is a main goal in the program. Since seed-related traits were highly correlated among themselves, it may be desirable to select that trait which is most economical to measure, probably seed yield panicle^{-1}, in order to improve other seed-related traits. To improve seed yield plant^{-1} it would be more efficient to select indirectly through earlier flowering or higher seed set, seed yield panicle^{-1}, or 100-seed weight, because of high correlated responses through these characters. Phenotypic correlations in this population were deceiving from a breeders point of view. Genetic and environmental causes of correlation combine together to give the phenotypic correlation through the following equation: $r_p = h_x h_y r_g + e_x e_y r_e$ (Falconer, 1989); where $e^2 = 1 - h^2$ (other terms have been described previously). When both characters x and y have low heritabilities, the phenotypic correlation is determined primarily by the environmental correlation, as was the case for almost all pairs of characters studied in this population. Since phenotypic correlations were largely determined by environmental correlations, they frequently differed greatly from the genetic correlations (Tables 5.5 and 5.6).

As often occurs in quantitative genetic studies, genetic parameter estimates may be somewhat biased in this study. The genetic parameters discussed in this paper are a function of environmental variability, so estimates may differ in other environments. Due to the nature of this research, the number of families was, by necessity, limited. This reduced the variation among families, consequently reducing family covariances, thus biasing heritability estimates downwards and somewhat altering genetic correlations. However, these families were the basis for a recurrent selection program currently in progress, where these estimates would be more applicable. Additionally,

heritabilities for seed-related traits could be biased downwards because only single-panicle measurements were taken, thus increasing within family variation.

CHAPTER 6
IMPROVING PEARL MILLET X ELEPHANTGRASS HYBRIDS VIA MASS SELECTION OR RECURRENT RESTRICTED PHENOTYPIC SELECTION

Introduction

As was mentioned in the previous chapter, further breeding of the pearl millet x elephantgrass hybrids will be required for future varietal development. Undesirable phenotypes are not uncommon in the breeding nurseries at the University of Florida. Substantial genetic variation was previously found in numerous traits evaluated (Diz and Schank, 1993), indicating significant potential for improvement. Mass selection, based on the unreplicated phenotypic evaluation of individual plants, is one of the oldest crop improvement techniques widely used. Usually highly heritable traits have responded well to mass selection, but characteristics with low heritabilities and complex inheritance have not responded as well to this procedure (Sprague, 1955; Burton, 1974). Recurrent restricted phenotypic selection (RRPS) is a modified form of mass selection, where a number of restrictions are imposed to increase the efficiency of the method (Burton, 1974). Plants are selected from a grid arrangement in the field to reduce the adverse effect of soil heterogeneity on selection; selected phenotypes are intermated in isolation in a polycross, thus imposing paternal as well as maternal selection; and inflorescences are intermated in close proximity in a greenhouse polycross, ensuring equal parental input as well as maximum recombination. Burton (1982) suggested several new restrictions to increase the efficiency of RRPS, but they

were somewhat specific for increasing dry matter yields in bahiagrass (*Paspalum notatum* Flugge.). Characteristics with low heritability values should respond better to this modified form of mass selection. On the other hand, mass selection is simple, inexpensive, and rapid, and adequate progress is usually obtained with highly heritable traits.

RRPS, as described by Burton (1974), involves detaching the inflorescences prior to stigma exertion from the selected plants in the field, and staging the polycross in a laboratory or greenhouse. In this way, problems inherent to field polycrosses such as isolation from foreign pollen sources, distances among plants (affecting random mating), maturity differences, unequal contribution of gametes from each parent to the next generation, and insufficient gene recombination can be avoided. The assumptions concerning a polycross are better met with the RRPS technique. Burton's procedure (1974) involved placing excised culms of bahiagrass in cans containing water. In a preliminary study, excised culms from several pearl millet x elephantgrass genotypes were placed in buckets containing water. Panicles were not able to fully exert from the sheaths of flag leaves and pollination and seed set were very poor. Adding sucrose to the water (20 g L^{-1}) as an energy source and hydroxyquinoline sulphate (0.2 g L^{-1}) to restrain fungal and bacterial development, allowed proper exertion and adequate seed set in the excised panicles (Diz, pers. comm.).

The objectives of this study were 1) to evaluate the feasibility of using excised panicles to develop isolated polycrosses in the greenhouse; 2) to compare the progress obtained after 2 cycles of mass selection (MS) and RRPS for a number of characteristics (seedling vigor, tillers $plant^{-1}$, leaf length and width, leaves $tiller^{-1}$, leafiness, plant height, panicle length, days to flowering, and seed production); and 3)

to obtain realized heritability values and compare these results with the expected heritability values described in chapter 5.

Materials and Methods

From the S_1 population described previously in chapters 4 and 5, 94 plants were selected in 1990 on the basis of desirable vegetative characteristics (high number of tillers and leafiness) and high seed production. An independent culling selection scheme was used, where plants selected surpassed the following values: plant score of 4 (from a scale of 1 to 10 which accounted for number of tillers and leafiness); 40% seed set; and 0.45 g of seed panicle^{-1}. Equal amounts of seed (in number) were collected from each of the 94 selected plants, and bulked together to form the base population. On 29 May 1991, 30 blocks containing 2 double rows 7 m in length were sowed at a rate of 0.5 g of seed (250-300 seeds) per row, using a belt planter at the Dairy Research Unit (DRU), University of Florida (39° 48' N latitude). Within a block, double rows were separated 2.70 m apart, with a 0.90 m separation within a double row. Early in the growing cycle plants were screened for vigor. The most vigorous seedling was selected from about every six seedlings. After this initial screening, approximately 8 plants remained per row, for a total of 32-34 plants per block. The total population of the nursery was approximately 1000 plants. Plants were fertilized in four split applications (29 May, 20 July, 20 Aug, and 24 Sept) for a total of 248-12-24 kg ha^{-1} of N-P_2O_5-K_2O. The area between rows was rototilled several times during the growing season and weeds within rows were removed manually. About one month before flowering, 5 to 6 plants per block were visually selected on the basis of high number of tillers, greater leafiness, and intermediate height. From this group, selection

emphasized early flowering and larger panicles, for a final selection of 3-4 plants per block. The total number of plants selected in 1991 was 93. A simplified diagram representing the selection procedures from 1990 to 1992 and the final progress evaluation in 1993 is represented in Fig. 6.1.

Panicle collection of selected plants was accomplished in two different ways. For the MS scheme, three mature panicles per selected plant were harvested in the field approximately 30 d after anthesis. Pollen source for these panicles was not controlled, so only maternal selection took place. For the RRPS scheme, three panicles per selected plant were excised when partially exerted from the flag leaf (stage prior to stigma exertion), leaving 40-60 cm of stem attached to the panicles. These were placed immediately into buckets of water and leaf blades were stripped to reduce transpiration. They were taken to a greenhouse and immature secondary panicles from axillary buds were removed from beneath the sheaths using a razor blade. Panicles were put into three large buckets containing a solution with 20 g L^{-1} sucrose and 0.2 g L^{-1} hydroxyquinoline sulphate. Panicles from the same plant were put into different buckets and within a bucket, panicles were placed at random. The panicles within each container were agitated every morning to ensure maximum cross pollination. This procedure maximized random mating among the different genotypes and isolation from foreign pollen sources, thus imposing paternal as well as maternal selection. Panicles were then harvested approximately 25-30 days after anthesis.

For both the MS and RRPS procedures mentioned above, panicles were dried for 48 hours at 35-40°C and then threshed with a Forsberg scarifier. Seed derived from the MS and RRPS procedures were bulked separately to constitute the improved MS and RRPS cycle 1 seed populations. By bulking the seed, indirect selection for seed

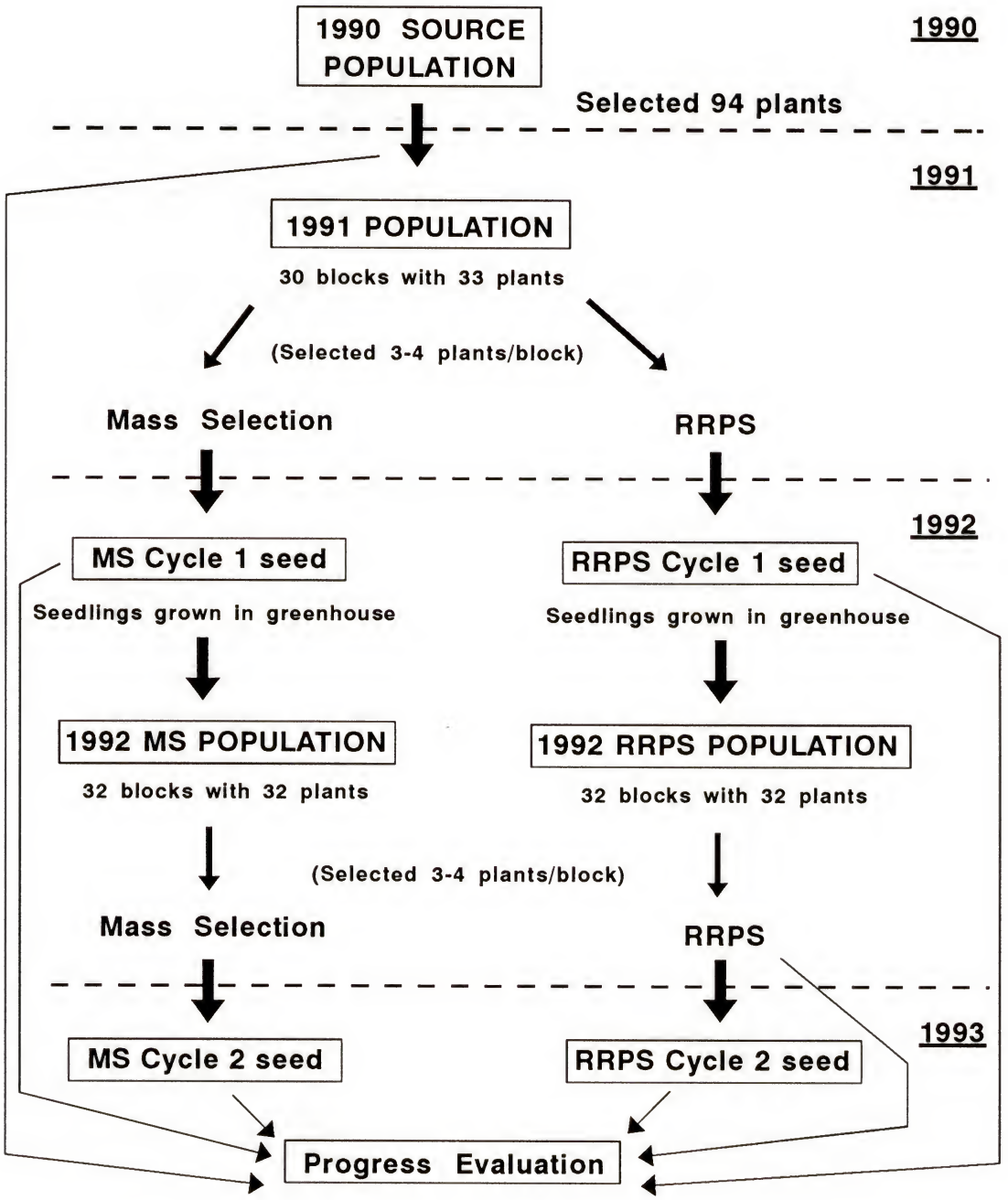

Fig. 6.1. A simplified diagram representing the selection procedures from 1990 to 1992, and the final progress evaluation in 1993.

production resulted because of the greater representation in the seed lots of those panicles which produced more seed. Seed production for 18 randomly-selected genotypes from the 93 plants selected was evaluated in more detail to determine differences between field and greenhouse seed production. Panicle length, seed yield panicle^{-1}, seeds panicle^{-1}, and 100-seed weight were measured on two panicles for each genotype x procedure combination, for a total of 72 panicles.

Improved MS and RRPS cycle 1 seed were sowed in a greenhouse in cavity trays containing Metromix 200® on 10 Mar 1992, for a total of 7000 seedlings for each population. Using a grid selection procedure, the most vigorous seedling out of every 6-7 seedlings was selected on 18 Mar 1992, for a total of 1150 plants per population. Seedlings were fertilized twice with aqueous solutions of Peters 20-20-20®, 15 and 30 days after seeding. They were also cut back to a stubble height of approximately 10 cm on 10 and 24 Apr 1992. Plants were transplanted into the field on 25 Apr 1992, using a similar design to that of 1991, except that two populations (MS 1992 and RRPS 1992) were planted. Each population consisted of 32 blocks containing 32 plants per block (four rows of eight plants each), for a total of approximately 1000 plants per population. Plants were spaced 0.90 m within a row, with distances between rows identical to those in 1991. Plants were fertilized in two split applications (25 April and 23 July) for a total of 168-42-84 kg ha^{-1} of N-P_2O_5-K_2O. The area between rows was rototilled several times during the growing season and weeds within rows were removed manually.

Using the same selection criteria as in 1991, 98 plants were selected from the RRPS 1992 population and 99 plants from the MS 1992 population. Only maternal selection was emphasized in the MS population, while maternal and paternal selection

was conducted in the RRPS population. Panicles from the selected plants in each population were collected and threshed as described in 1991. The seed obtained from the selected plants in each population was bulked separately to constitute the improved MS cycle 2 and RRPS cycle 2 seed populations.

Progress obtained from the MS and RRPS procedures in 1991 and 1992 was evaluated in 1993. Six entries were included in this evaluation: the source population, MS cycles 1 and 2, RRPS cycles 1 and 2, and the RRPS cycle 1 selections (which when polycrossed, resulted in the RRPS cycle 2 seed). This last entry was included to calculate realized heritability values for the traits under study. On 30-31 Mar 1993, seeds from the first five entries (source, MS cycle 1, MS cycle 2, RRPS cycle 1, and RRPS cycle 2) were sowed in plastic cavity trays containing Metromix 200® in a randomized block design with 3 replications. For each entry within a replication, 36 random seedlings were evaluated for seedling vigor. Height of seedlings (measured as the distance between the soil surface and the top of extended leaves) was measured 8 and 18 days after sowing. Additionally, the 100-seed weight mean for each entry was obtained by weighing four replications of 100 seeds. From each entry, 98 seedlings were then randomly selected and transplanted into the field on 19-20 May 1993, in a design described as a spaced-plant-population-progress (SPPP) test (Burton, 1985). It consisted of a randomized complete block design with one seedling from each entry placed at random in each block, providing 98 blocks or replications for the test. Additionally, the 98 plant selections which gave rise to the RRPS cycle 2 seeds were maintained clonally from the previous year, and also placed randomly in each block. In this test, 98 blocks were implemented instead of 100 because there were only 98 RRPS cycle 1 selections. Each block consisted of 6 plants in a row, spaced 1.35 m

between plants and 2.70 m between rows (blocks). Plants were fertilized in three split applications (23 May, 20 July, and 4 Sept) for a total of 234-59-117 kg ha^{-1} of N-P_2O_5-K_2O. Individual plants in the test were evaluated for the following characteristics: tillers $plant^{-1}$, leaf length and width, leaves $tiller^{-1}$, plant height, days to flowering, panicle length, seed yield $panicle^{-1}$, and seed yield $plant^{-1}$. Two mature leaf blades per plant were sampled from nodes at mid-height of the plant, for both leaf length and width measurements. One representative tiller per plant was counted for number of leaves $tiller^{-1}$. A 'leafiness' index was calculated by multiplying leaf length x leaf width x leaves $tiller^{-1}$ x tillers $plant^{-1}$. Plant height was measured from the soil surface to the top of inflorescences. Days to flowering was calculated as the number of days from transplanting into the field (19 May) until three panicles were fully exerted from their flag leaves. Panicle length and seed yield $panicle^{-1}$ were measured on one primary panicle $plant^{-1}$. Seed yield $plant^{-1}$ was estimated by multiplying seed yield $panicle^{-1}$ x tillers $plant^{-1}$. Since each tiller usually produces one primary panicle and several secondary panicles, this estimation of seed yield $plant^{-1}$ only accounted for seed produced by primary panicles. Because of an unexpected early freeze on 2-3 Nov 1993, mature panicles for seed were collected from only 145 plants (19 source population plants; 18 MS cycle 1 plants; 25 RRPS cycle 1 plants; 25 MS cycle 2 plants; 24 RRPS cycle 2 plants; and 34 RRPS cycle 1 selections). For this reason, entries were not adequately sampled for seed yield $panicle^{-1}$ and seed yield $plant^{-1}$, and population means could be somewhat biased.

For both the seedling vigor experiment in the greenhouse and the SPPP test in the field, analyses of variance were performed using the general linear model procedure of the Statistical Analysis System (SAS Institute Inc., 1985). Differences among entries

for the characteristics under study were identified with this procedure. Fisher's protected LSD test was used in the greenhouse and SPPP experiments when the F-test for entries showed significance at the 5% level of probability. Progress due to the MS and RRPS procedures were compared. For each entry, the coefficients of variation (CV) for all characteristics were calculated. CV values were obtained to assess the existing variability within each population and the progress that could be expected in the following cycle of selection. Realized heritability (h^2) values for the traits evaluated in the field were obtained through the following equation:

$$\text{Realized } h^2 = \frac{\text{RRPS cycle 2 - RRPS cycle 1}}{\text{RRPS cycle 1 selections - RRPS cycle 1}}$$

where the values for each entry stated in the equation are the population means for each trait evaluated. Realized heritability values were compared with the expected heritability values discussed in chapter 5.

Results

The first study involved evaluating seed production from panicles in the field versus excised panicles grown in a solution containing sucrose and hydroxyquinoline sulphate in a greenhouse. Means for panicle length, seeds panicle^{-1}, 100-seed weight, and seed yield panicle^{-1} for 18 of the 93 genotypes selected in 1991 are shown in Table 6.1. Differences in panicle length were not found between field panicles and excised cultured panicles. However, seeds panicle^{-1} dropped 49% and 100-seed weight was reduced 25% when comparing excised panicles with field panicles. The end result was a reduction in seed yield panicle^{-1} of 63%. Nevertheless, for polycross purposes in a

Table 6.1. Comparison between panicles maturing in the field versus excised panicles grown in a solution containing 20 g L^{-1} of sucrose and 0.2 g L^{-1} of hydroxyquinoline sulphate in a greenhouse. Means for panicle length, seeds $panicle^{-1}$, 100-seed weight, and seed yield $panicle^{-1}$ for 18 randomly selected genotypes from the 93 plants selected in 1991 are shown.

Treatment	Panicle length	Seeds $panicle^{-1}$	100-seed weight	Seed yield $panicle^{-1}$
	cm	no.	mg	mg
Field panicles	26.0	577	181	1098
Excised panicles	25.8	297	135	406
Reduction (%)†	1	49	25	63
Significance‡	NS	**	**	**

†: Reduction (%) calculated as [(Field panicles-Excised panicles)/Field panicles] x 100.
‡ NS, **: Non-significant differences between treatments and significant at the P=0.01 level, respectively.

breeding program, this represents a sufficient amount of seed. The greenhouse polycross methodology seemed to be very efficient in avoiding problems inherent to field polycrosses.

Table 6.2. shows mean seedling vigor values (height of seedlings 8 d and 18 d after sowing) and 100-seed weight for the five entries evaluated in the greenhouse in 1993. Because the seed representing each entry was produced in different years (1990, 1991, or 1992) and environments (field or greenhouse), this data was confounded by these effects. For this reason, RRPS seed (cycles 1 and 2) had low seed weight, since they were produced by excised panicles in the greenhouse. Despite differences in 100-seed weight, seedling vigor (8 d and 18 d measurements) was not different among entries, except for RRPS cycle 2 which had the lowest means. This could be explained by its low seed weight, which could merely be due to the environment in which seed development took place. An interesting occurrence is that despite the low seed weight of RRPS cycle 1, the seedling vigor of this entry was not different from the other entries. This could indicate some genetic improvement when compared to the source. However, no real evidence of seedling vigor improvement could be derived from this experiment.

Tables 6.3. and 6.4. present mean values, percent change relative to the source population, and CV's for the characteristics evaluated in the 1993 SPPP test. MS and RRPS cycle 1 were not different from the source population, except for leaves tiller^{-1} in RRPS cycle 1. RRPS cycle 1 tended to be numerically superior to MS cycle 1 for the majority of traits, but differences between these two procedures were not significant. Differences from the source population became apparent after the second cycle of selection, primarily for RRPS. The RRPS cycle 2 entry was greater than the source

Table 6.2. Mean 100-seed weight and seedling vigor values (height of seedlings 8 and 18 d after sowing) for the five pearl millet x elephant-grass entries [source population, mass selection (MS) cycles 1 and 2, and recurrent restricted phenotypic selection (RRPS) cycles 1 and 2] evaluated in the greenhouse in 1993.

Entries	100-seed weight	Seedling height	
		8 d	18 d
	mg	cm	
Source	190 b†	2.99 a	16.9 a
MS Cycle 1	213 a	3.24 a	17.3 a
RRPS Cycle 1	165 c	3.00 a	16.8 a
MS Cycle 2	188 b	3.04 a	16.9 a
RRPS Cycle 2	149 d	2.55 b	14.8 b

† Means followed by the same letter within columns are not different ($p<0.05$), according to Fisher's Protected LSD.

Table 6.3. Mean values and population variability for the leaf and tiller characteristics in the pearl millet x elephantgrass entries [source population, mass selection (MS) cycles 1 and 2, recurrent restricted phenotypic selection (RRPS) cycles 1 and 2, and RRPS cycle 1 selections] evaluated in the spaced-plant-population-progress test in 1993.

Entry	Leaf length			Leaf width			Leaves tiller^{-1}			Tillers plant^{-1}			Leafiness†		
	Actual	Relative‡	CV	Actual	Relative	CV	Actual	Relative	CV	Actual	Relative	CV	Actual	Relative	CV
	cm	------ % -----		cm	----- % -----		no.	----- % -----		no.	----- % -----		m^2	----- % ----	
Source	92.5	100	15	4.46	100	19	12.6	100	24	31.1	100	37	17.4	100	58
MS cycle 1	93.1	101	16	4.37	98	24	12.7	100	20	33.5	108	35	17.6	101	51
RRPS cycle 1	92.5	100	16	4.49	101	21	13.3	106	20	33.7	108	39	19.2	111	55
MS cycle 2	94.5	102	16	4.68	105	20	13.4	106	19	32.8	106	30	20.7	119	52
RRPS cycle 2	95.6	103	14	4.82	108	18	13.5	107	21	33.9	109	28	21.6	124	47
Selections ¶	101.1	109	11	4.78	107	14	13.7	109	14	36.1	116	23	24.0	138	33
LSD (0.05)	3.8	4	-	0.25	6	-	0.7	5	-	2.7	8.5	-	2.6	15	-

† Leafiness calculated as: leaf length x leaf width x leaves tiller^{-1} x tillers plant^{-1}.
‡ Relative to source population.
¶ RRPS cycle 1 selections.

Table 6.4. Mean values and population variability for plant height, days to flowering, panicle length, and seed characteristics in the pearl millet x elephantgrass entries [source population, mass selection (MS) cycles 1 and 2, recurrent restricted phenotypic selection (RRPS) cycles 1 and 2, and RRPS cycle 1 selections] evaluated in the spaced-plant-population-progress test in 1993.

Entry	Plant height			Days to flowering			Panicle length			Seed yield panicle^{-1}			Seed yield plant^{-1}†		
	Actual	Relative‡	CV	Actual	Relative	CV	Actual	Relative	CV	Actual	Relative	CV	Actual	Relative	CV
	m	----- % ------		days	----- % -----		cm	----- % -----		mg	----- % -----		g	----- % ----	
Source	3.30	100	18	153.3	100	9	21.2	100	22	255	100	80	8.5	100	86
MS cycle 1	3.32	101	19	152.0	99	8	21.1	100	18	371	145	84	12.8	151	84
RRPS cycle 1	3.31	100	19	151.4	99	9	21.6	102	21	322	126	116	11.7	138	117
MS cycle 2	3.38	102	18	150.6	98	9	21.8	103	18	355	139	73	12.1	143	95
RRPS cycle 2	3.48	105	16	148.7	97	8	23.2	109	18	355	139	91	13.8	163	103
Selections ¶	3.68	111	8	144.2	94	5	25.0	118	13	477	187	77	18.1	214	85
LSD (0.05)	0.16	4	-	3.5	2	-	1.2	5	-	NS	NS	-	NS	NS	-

† Seed yield plant^{-1} calculated as: seed yield panicle^{-1} x tillers plant^{-1}.
‡ Relative to source population.
¶ RRPS cycle 1 selections.

population for leaf width, leaves tiller^{-1}, tillers plant^{-1}, leafiness (24% increase), plant height, and panicle length; and flowered earlier than the source population. MS cycle 2 was greater than the source population only for leaves tiller^{-1} and leafiness. After two cycles of selection, RRPS was more effective than MS in improving the traits under selection. This was expected since both male and female selection took place in RRPS, whereas only female selection was implemented in MS. Because of the low sampling numbers (low degrees of freedom) and the high variability encountered in seed yield panicle^{-1} and seed yield plant^{-1}, differences were not significant among entries for these two traits. However, percent change due to selection relative to the source population was greatest in these traits. After two cycles of MS and RRPS, seed yield panicle^{-1} increased 39% with either procedure. The value for MS cycle 1 was still greater (45% increase), but this value could be biased because of the low number of plants evaluated for seed yield panicle^{-1}. For seed yield plant^{-1}, there was a 43 and 63% increase relative to the source population, after two cycles of MS and RRPS, respectively. The greater relative improvement in these characteristics would tend to confirm those results obtained in chapter 5, where predicted responses to selection were greatest for seed-related characters. Means for the RRPS cycle 1 selections (selected RRPS plants in 1992) were superior to all other entries, except for leaf width. These were the plants selected from the RRPS cycle 1 population, which when polycrossed, resulted in the RRPS cycle 2 seed. RRPS cycle 2 means were expected to be lower than their parental means, because the population means tend to regress back to the RRPS cycle 1 means.

Overall, population CV's fluctuated somewhat but remained fairly close to those obtained for the source population. Significant losses of genetic variation due to

selection were not evidenced, as indicated by these CV values. As would be expected within selected plants, the RRPS cycle 1 selections expressed lower variability than the RRPS cycle 1 and 2 populations.

From the entries RRPS cycle 1, RRPS cycle 2, and RRPS cycle 1 selections, realized heritabilities were calculated and are shown in Table 6.5. The heritability for leaf width resulted in a value greater than one (1.14), which is not genetically possible. However, it would show that this character is highly heritable. The other realized heritabilities ranged from 0.11 for tillers plant^{-1} to 0.5 for the leafiness index. Values tended to be in the 0.3-0.5 range, being usually higher than the estimated values reported in Chapter 5. Several problems which may have been responsible for lowering these estimated values were discussed at the end of Chapter 5. The realized heritability values obtained were very promising, showing that improvement through selection can be very effective in these interspecific hybrids.

Discussion

Several grass species have been reported to successfully produce seed from detached culms or inflorescences (Ascher et al., 1987; Burton, 1974; Donovan and Lee, 1977; Grau, 1982; Haack et al., 1987; Weisner and Grabe, 1972; Wofford et al., 1986). This procedure was successful with the *Pennisetum* hybrids when panicles were placed in a solution containing 20 g L^{-1} sucrose and 0.2 g L^{-1} hydroxyquinoline sulphate. The reduction in seeds panicle^{-1} and 100-seed weight in excised panicles coincided with studies in other species where the production of seed through the detached culm or inflorescence technique was usually lower than that for intact inflorescences under field conditions (Wofford et al., 1986, and references in this

Table 6.5. Realized heritability values for the characteristics evaluated in the spaced-plant-population-progress test in 1993.

Characteristics	Realized heritability†
Leaf length	0.37
Leaf width	1.00‡
Leaves tiller^{-1}	0.33
Tillers plant^{-1}	0.11
Leafiness	0.50
Plant height	0.47
Days to flowering	0.37
Panicle length	0.46
Seed yield panicle^{-1}	0.21
Seed yield plant^{-1}	0.33

† Realized heritability = $\frac{\text{RRPS cycle 2 - RRPS cycle 1}}{\text{RRPS cycle 1 selections - RRPS cycle 1}}$

‡ Value greater than 1.00 but assumed to be equal to 1.00.

paper). Nevertheless, adequate amounts of seed for breeding purposes were produced through this procedure.

After two cycles of selection, RRPS was more effective than MS in improving the traits under selection. RRPS cycle 1 and MS cycles 1 and 2 were not different from the source population for most traits because selection for multiple traits took place. When selecting for multiple traits in each generation, the intensity of selection for each individual trait is greatly reduced, thus reducing improvement on an individual trait basis. Nevertheless, after two cycles of RRPS, the majority of traits evaluated were improved when compared to the source population. The excised panicle technique was necessary for carrying out the more efficient RRPS procedure in which both male and female gametes were selected. However for most traits, RRPS improvement was not twice as effective as the improvement through MS. For example, leafiness was increased 19% after two cycles of MS and 24% after two cycles of RRPS (Table 6.3). For this leafiness index, RRPS was 27% superior to MS rather than 100% superior. If RRPS were twice as effective as MS, improvement after two cycles of RRPS should have been 38% (19% x 2). Improvement through RRPS was over 100% more effective than the improvement through MS only for plant height (125% greater) and panicle length (230% greater). The other traits ranged from 0% greater in seed yield panicle^{-1} to 70% greater in days to flowering, when comparing the relative improvement of RRPS over MS after two cycles of selection. A possible explanation is that pollen fertilizing the ovaries of selected plants in the MS populations were probably derived from plants which overall had a higher mean for the traits analyzed than the mean of the population. Plants with higher numbers of tillers produced more panicles and hence more pollen for fertilization; later flowering plants probably did not get a chance

to fertilize the selected plants in the MS populations which were selected for earliness; taller, more leafy plants tend to flower earlier and probably contributed more male gametes in the fertilization process than shorter, less leafy plants. Some degree of indirect selection for pollen in the MS populations does naturally occur and it is incorrect to assume that improvement through RRPS will double that of MS.

The CV values obtained showed that there were no significant losses in the variability of the populations after selection, indicating that further improvement through MS or RRPS should be expected in future cycles of selection. This was also supported by the realized heritability values which mostly ranged between 0.3 and 0.5. If higher intensities of selection were implemented on the characteristics with greatest economic value, improvement should be very satisfactory in each generation. The characteristics to select for will vary according to the expected end use of the variety being developed. The RRPS procedure is recommended over the MS procedure described in this chapter. The work (man-hours) involved in RRPS was not dramatically greater than that of the MS procedure, but the effectiveness of RRPS was clearly superior.

CHAPTER 7
GENERAL SUMMARY AND CONCLUSIONS

A series of experiments were conducted with pearl millet x elephantgrass hexaploid hybrids over a period of three years. The following overall objectives were pursued: i) evaluating possible management procedures for mechanizing seed harvest; ii) improving the efficiency of breeding programs for this crop; and iii) evaluating the success of different selection methodologies for multiple traits. The experiments were conducted at the Dairy Research Unit, University of Florida, during the years 1990 to 1993.

Seed Related Characteristics as Influenced by Defoliation Management

To meet the first objective, an experiment was conducted where three defoliation treatments (no cuts, two cuts, and three cuts per year) were imposed on four different genotypes during 1991 and 1992. Traits evaluated included plant height, days to flowering, seed yield components, seed yield plant^{-1}, seed germination, and plant survival. The goal of achieving a reduction in the height and biomass of the plants, while maintaining adequate seed yield and seed quality, was attained with two cuts per year (mid June and beginning of August). In 1991, plants cut twice yielded 28% more seed on average than uncut plants. In 1992, there was a 44% reduction in seed yield of plants cut twice, primarily due to a reduction in primary panicles plant^{-1}. Timing of fertilizer applications during this second year may have played an important role in this

reduction. Seed germination and persistence of plants cut twice per year was not affected. Cutting plants three times per year (last cut in mid-September) proved to be very detrimental for seed production. Seed yield plant^{-1} dropped 77 and 98% in 1991 and 1992, respectively, compared to uncut plants. This was primarily due to reductions in primary panicles plant^{-1} and seeds panicle^{-1}. Defoliating plants in September would not be recommended if seeds were to be harvested that fall. Adequately-timed two cuts per year would seem a viable alternative for mechanizing seed harvest. This practice reduced the height of panicles and the biomass of the plants while maintaining good seed production and seed quality.

Improving the Efficiency of Pearl Millet x Elephantgrass Breeding Programs

To meet the second objective, data collected from an experiment containing 7 selfed (S_1) families were analyzed to obtain single plant heritability estimates, genetic and phenotypic correlations, and predicted responses to selection. Traits evaluated in this experiment included leaf length and width, tillers plant^{-1}, plant height, days to flowering, panicle length, panicles plant^{-1}, seed set, seeds panicle^{-1}, seed yield panicle^{-1}, seed yield plant^{-1}, and 100-seed weight. Path-coefficient analyses of seed yield components were also evaluated in this experiment to measure the direct and indirect effects of each component on total seed yield plant^{-1}.

Single plant heritability estimates were very low to moderate for the vegetative and reproductive traits studied, ranging from 0.02 to 0.30. Despite these relatively low heritability values, predicted responses to selection for reproductive traits were high due to large phenotypic variation. Improvement through phenotypic selection should be satisfactory in these traits. Genetic correlations among vegetative and reproductive

traits were analyzed, in order to understand the effects on different traits when selecting for specific traits. Seed-related traits were highly correlated among themselves. Therefore to improve all seed-related traits, it would be desirable to select only that trait which is most economical to measure (probably seed yield panicle^{-1}). To improve seed yield plant^{-1}, it seemed more efficient to select indirectly through earlier flowering or other seed-related traits rather than directly for seed yield plant^{-1}. Phenotypic correlations in this population were inconsistent from a breeders point of view. Most phenotypic correlations were determined primarily by the environmental correlation because of a large environmental influence on these traits. For this reason, phenotypic correlations usually differed greatly from the genetic correlations.

Path-coefficient analyses of seed yield components indicated that selection for the components seeds panicle^{-1} and 100-seed weight would be most effective for improving seed yield plant^{-1}. Since seed yield panicle^{-1} encompasses these two components and is easier to measure, selection for this trait would be recommended. Due to large environmental influence on the phenotypic correlations, path analysis utilizing genetic correlations was more effective in developing selection criteria.

Evaluating the Success of Mass Selection vs. Recurrent Restricted Phenotypic Selection

Mass selection (MS) and recurrent restricted phenotypic selection (RRPS) were implemented on a population for two cycles of selection and then evaluated for progress. Selection in the greenhouse and field emphasized higher seedling vigor, leafiness, tillers plant^{-1}, panicle length, intermediate height, and early flowering. Traits evaluated for progress in 1993 included leaf length and width, leaves tiller^{-1}, tillers plant^{-1}, leafiness, plant height, days to flowering, panicle length, seed yield panicle^{-1},

and seed yield plant^{-1}. After two cycles of selection, RRPS was more effective than MS in improving the traits under selection. The excised panicle technique was necessary for carrying out the more efficient RRPS procedure in which both male and female plants were selected. However, for most traits, RRPS improvement was not twice as effective as the improvement through MS. The CV values obtained showed that there were no significant losses in the variability of the populations after selection, indicating that further improvement through MS or RRPS should be expected in future cycles of selection. Realized heritability values ranged mostly between 0.3 and 0.5. These observed values were larger than the previously estimated heritability values. Because selection emphasized numerous traits, the intensities of selection for each individual trait varied and were low. If higher intensities of selection were implemented on a few characteristics with greatest economic value, improvement should be very satisfactory in each generation. The RRPS procedure is recommended over the MS procedure because of its greater effectiveness in improving characteristics.

Suggestions for Future Research and Varietal Development

Increased seed yield and seed quality are especially important in these pearl millet x elephantgrass hexaploid hybrids. Elephantgrass varieties which are very adequate for forage and biomass production are already available to farmers in the U.S. However, they are not being used commercially because they must be propagated vegetatively. This has served as a deterrent to its adoption because of the high labor requirements and the high cost associated with the establishment. For this reason, adequate seed yield and seed quality are essential to the success of these interspecific hybrids. To date, endeavors of producing triploid pearl millet x

elephantgrass seed on a commercial scale have failed. Seed yield and quality have not been adequate. Developing varieties at the hexaploid level may therefore be the solution.

Future varietal development should emphasize selecting for higher seed yield and seed quality, among other important traits. Depending on the end use of the variety, the characters selected for will vary. However, adequate seed yield should always be a primary goal. The research described has shown that there is large room for improvement. Selecting for higher seed yield panicle^{-1} would be suggested because it is relatively easy to measure and is highly correlated with seed yield plant^{-1}. RRPS would be preferred rather than mass selection because of its greater effectiveness. Other important traits such as persistence will also be essential for the success of these hybrids. Macoon (1992) and Spitaleri (1992) have discussed the importance of persistence in these hybrids, and the need for improvement. There would seem to be large genetic variation for this trait, as evidenced by the existing populations in old breeding nurseries. The genotypes used in the seed production study (Chapter 3) in which different defoliation treatments were imposed during two years, showed very adequate survival. To date there is still over 80% survival of those plants cut three times per year. Future research should try to characterize the existing genetic variability for persistence, and the most appropriate way to select for it, either directly or indirectly. Rhizome mass and total non-structural carbohydrate (TNC) concentration are usually correlated with persistence and seem logical traits to select for. However, measuring these traits in a large breeding nursery would not be practical. Therefore, other traits which are easier to measure should be analyzed for their correlation with persistence. Tillers plant^{-1} may be an appropriate indicator of persistence. Since it has

been selected for during these years, persistence of the hybrids on a population basis may have improved. This could be evaluated in the spaced-plant-population-progress test at the Dairy Research Unit (University of Florida) in 1994 and 1995. Defoliation could be imposed on this population, and the persistence measured.

It would also be desirable to bring new germplasm into the breeding program. Although there is large genetic variation in the individual traits measured, the initial base of the breeding population is narrow. This may compromise future improvement of the interspecific hybrids.

REFERENCE LIST

Aken'Ova, M.E., and H.R. Chheda. 1981. Seed production for the establishment of *Pennisetum americanum* x *P. purpureum* F_1 hybrid pastures. p. 261-262. *In* J.A. Smith and V.W. Hays (eds.) Proc. XIV Intern. Grass. Cong., Lexington, Kentucky, 15-24 June 1981. Westview Press, Inc., Boulder, Colorado.

Aldrich, D.T.A. 1959. The effect of grazing management on the response of winter wheat to spring defoliation. Emp. J. Exp. Agric. 27: 10-16.

Andrade, R.P., and D. Thomas. 1981. Pesquisas em avaliação de pastagens e produção de sementes de forrageiras no centro de pesquisa agropecuaria dos cerrados. p 82. *In* R.B. Madeiros, C. Nabinger, and J.C.D. Saibro (ed.) Produção e technologia de sementes de forrageiras tropicais e subtropicais. Promoção COTRIJUI/UFRGS/FAO. Porto Alegre e IJUI/RS/Brasil.

Ascher, P.D., B.A. Ruemmele, and D.B. White. 1987. Factors affecting seed set from detached *Poa* spp. inflorescences. Agron. Abst. 79: 132.

Bogdan, A.V. 1966. Plant introduction, selection, breeding and multiplication. p. 75-88. *In* W. Davies and C.L. Skidmore (eds.). Tropical pastures. Faber and Faber Limited, London, Great Britain.

Bogdan, A.V. 1977. Tropical pasture and fodder plants. Trop. Agric. Series, Longman Group Ltd., London. 475 pp.

Brunken, J.N. 1977. A systematic study of *Pennisetum* sect. *Pennisetum* (Gramineae). Amer. J. Bot. 64: 161-176.

Burton, G.W. 1942. A cytological study of some species in the tribe Paniceae. Amer. J. Bot. 29: 355-359.

Burton, G.W. 1944. Hybrids between napier grass and cattail millet. J. Hered. 35: 227-232.

Burton, G.W. 1958. Cytoplasmic male sterility in pearl millet (*Pennisetum glaucum* (L.) R.Br. Agron. J. 50: 230-231.

Burton, G.W. 1965a. Pearl millet Tift 23A released. Crops Soils 18: 19.

Burton, G.W. 1965b. Male-sterile pearl millet Tift 18A released. Crops Soils 18: 19.

Burton, G.W. 1967. Pearl millets Tift 23DA and 23DB released. Georgia Agric. Res. 9: 6.

Burton, G.W. 1974. Recurrent restricted phenotypic selection increases forage yields of Pensacola bahiagrass. Crop Sci. 14: 831-835.

Burton, G.W. 1982. Improved recurrent restricted phenotypic selection increases bahiagrass forage yields. Crop Sci. 22: 1058-1061.

Burton, G.W. 1985. Spaced-plant-population-progress test. Crop Sci. 25: 63-65.

Burton, G.W., and D.S. Athwal. 1967. Two additional sources of cytoplasmic male-sterility in pearl millet and their relationship to Tift 23A. Crop Sci. 7: 209-211.

Burton, G.W., and D.S. Athwal. 1968. Reciprocal maintainer-restorer relationship between A_1 and A_2 sterile cytoplasms facilitates millet breeding. Crop Sci. 8: 632-634.

Burton, G.W., and J.B. Powell. 1968. Pearl millet breeding and cytogenetics. Adv. Agron. 20: 49-89.

Christiansen, S., T. Svejcar, and W.A. Phillips. 1989. Spring and fall cattle grazing effects on components and total grain yield of winter wheat. Agron. J. 81: 145-150.

Crow, J.F., and M. Kimura. 1970. An introduction to population genetics theory. Harper & Row, Publishers. New York, NY.

Dann, P.R., A. Axelsen, S. Dear, E.R. Williams, and C.B.H. Edwards. 1983. Herbage, grain, and animal production from winter-grazed cereal crops. Aust. J. Exp. Agric. Anim. Husb. 23: 154-161.

Davies, O. 1968. The origins of agriculture in West Africa. Curr. Anthropology 9: 479-482.

de Wet, J.M.J. 1987. Pearl millet (*Pennisetum glaucum*) in Africa and India. *In* Proc. Intern. Pearl Millet Workshop, 7-11 April 1986, ICRISAT Center, India. Patancheru, A.P. 502 324, India.

Dewey, D.R., and K.H. Lu. 1959. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agron. J. 51:515-518.

Diz, D.A., and S.C. Schank. 1991. Seed and seedling characterization of pearl millet x napiergrass hexaploid hybrids. Proc. Soil Crop Sci. Soc. Florida 50: 69-75.

Diz, D.A., and S.C. Schank. 1993. Characterization of seed producing pearl millet x elephantgrass hexaploid hybrids. Euphytica 67: 143-149.

Donovan, G.R., and J.W. Lee. 1977. The growth of detached wheat heads in liquid culture. Plant Sci. Lett. 9: 107-113.

Dujardin, M., and W.W. Hanna. 1985. Cytology and reproductive behaviour of pearl millet-napiergrass hexaploids x *Pennisetum squamulatum* trispecific hybrids. J. Hered. 76: 382-384.

Dujardin, M., and W.W. Hanna. 1986. An apomictic polyhaploid obtained from a pearl millet x *Pennisetum squamulatum* apomictic interspecific hybrid. Theor. Appl. Genet. 72: 33-36.

Falconer, D.S. 1989. Introduction to quantitative genetics. 3rd ed. Longman Scientific and Technical, Essex, England.

Ferraris, R. 1973. Pearl millet (*Pennisetum typhoides*). Commonwealth Agric. Bureaux, Farnham Royal, UK. 70pp.

Fonseca, S., and F.L. Patterson. 1968. Yield component heritabilities and interrelationships in winter wheat (*Triticum aestivum* L.). Crop Sci. 8:614-617.

Gardner, C.S., and G.M. Prine. 1987. Phytomass yield of elephantgrass as affected by fertilizer nitrogen and cool-season legume intercrop. Proc. Soil Crop Sci. Soc. Florida 46: 46-51.

Gildenhuys, P.J. 1950. A new fodder grass - A promising cross between babala and napier fodder. Farming in South Africa 15: 189-191.

Gildenhuys, P.J., and K. Brix. 1964. Genically controlled variability of chromosome number in *Pennisetum* hybrids. J. Hered. 19: 533-542.

Gonzalez, B., and W.W. Hanna. 1984. Morphological and fertility responses in isogenic triploid and hexaploid pearl millet x napiergrass hybrids. J. Hered. 75: 317-318.

Grau, I. 1982. Nutrient solution culture for winter rye ears. Arch. Zuchtungsforsch 12: 245-247.

Gravois, K.A., S.B. Milligan, and F.A. Martin. 1991. Additive genetic effects for sugarcane yield components and implications for hybridization. Trop. Agric. 68:376-380.

Gupta, V.P., and D.S. Athwal. 1966. Genetic variability, correlation, and selection indices of grain characters in pearl millet. J. Res. Punjab Agric. Univ. 3: 111-117.

Haack, A., E. Kappler, and G. Zenke. 1987. Culturing of barley and rye ears in culturing solutions. Arch. Zuchtungsforsch 17: 59-62.

Hanna, W.W. 1981. Method of reproduction in napiergrass and in the 3X and 6X alloploid hybrids with pearl millet. Crop Sci. 21: 123-126.

Hanna, W.W. 1987. Utilization of wild relatives of pearl millet. *In* J.R. Witcombe and S.R. Beckerman (eds.). Proc. Intern. Pearl Millet Workshop, 7-11 April, 1986. ICRISAT Center, India. Patancheru, A.P. 502 324, India.

Hanna, W.W., and W.G. Monson. 1980. Yield, quality, and breeding behavior of pearl millet x napiergrass interspecific hybrids. Agron. J. 72: 358-360.

Hanna, W.W., and W.G. Monson. 1988. Registration of dwarf Tift N75 napiergrass germplasm. Crop. Sci. 28: 870-871.

Hanna, W.W., M. Dujardin, P. Ozias-Akins, and L. Arthur. 1992. Transfer of apomixis in *Pennisetum*. p 30-33. *In* E.H. Jones Jr. and J.P. Miksche (eds.). Proc. Apomixis Workshop, 11-12 February, 1992. Atlanta, Georgia. US Dep. of Agric., ARS.

Harlan, J.R. 1971. Agricultural origins: centers and noncenters. Science 174: 468-474.

Harvey, W.R. 1990. Harvey's least-squares program user's guide. 1990 ed. Columbus, Ohio.

Holliday, R. 1956. Fodder production from winter-sown cereals and its effect upon grain yield. Field Crop Abstr. 9: 129-135,207-213.

Humphreys, L.R., and F. Riveros. 1986. Tropical pasture seed production. FAO Plant Production and Protection Paper #8, Rome.

Ivanovic, M., and K. Rosic. 1985. Path coefficient analysis for three stalk traits and grain yield in maize (*Zea mays* L.). Maydica 30:233-239.

Jauhar, P.P. 1968. Inter- and intra-genomal chromosome pairing in an inter-specific hybrid and its bearing on the basic chromosome number in *Pennisetum*. Genetica 39: 360-370.

Jauhar, P.P. 1981. Cytogenetics and breeding of pearl millet and related species. Alan R. Liss, Inc. New York, NY.

Jauhar, P.P., and U. Singh. 1969. Amphidiploidization induced by decapitation in an interspecific hybrid of *Pennisetum*. Curr. Sci. 38: 420-421.

Kang, M.S., J.D. Miller, and P.Y.P. Tai. 1983. Genetic and phenotypic path analyses and heritability in sugarcane. Crop Sci. 23:643-647.

Khan, M.D. and H. Rahman. 1963. Genome relationship and chromosome behaviour in the allotriploid hybrid of *Pennisetum typhoides* and *P. purpureum*. W. Pak. J. Agric. Res. 1: 61-65.

Kilcher, M.R. 1982. Effect of cattle grazing on subsequent grain yield of fall rye (*Secale cereale* L.) in southwestern Saskatchewan. Can. J. Plant Sci. 62: 795-796.

Krishnaswamy, N. 1962. Bajra: *Pennisetum typhoides* S&H. Indian Council of Agric. Res. Cereal Crop Ser. II.

Krishnaswamy, N., and V.S. Raman. 1949. A note on the amphidiploid of the hybrid of *Pennisetum typhoides* Stapf and Hubbard x *P. purpureum* Schumach. Current Sci. 18: 15-16.

Krishnaswamy, N., and V.S. Raman. 1954. Studies on the interspecific hybrid of *Pennisetum typhoides* Stapf and Hubb. x *P. purpureum* Schumach. III. The cytogenetics of the colchicine-induced amphidiploid. Genetica 27: 253-272.

Krishnaswamy, N., and V.S. Raman. 1956. Studies on the interspecific hybrid of *Pennisetum typhoides* x *P. purpureum*. IV. The cytogenetics of the allotetraploids. Genetica 28: 345-360.

Li, C.C. 1975. Path analysis - a primer. The Boxwood Press, Pacific Grove, CA.

Macoon, B. 1992. Defoliation effects on yield, persistence, and quality-related characteristics of four *Pennisetum* forage genotypes. M.S. thesis. Univ. of Florida, Gainesville.

Mishra, M.L., and B.N. Chatterjee. 1968. Seed production in the forage grasses *Pennisetum polystackyon* and *Andropogon gayanus* in the indian tropics. Trop. Grassl. 2: 51-56.

Mislevy, P., R.S. Kalmbacher, A.J. Overman, and F.G. Martin. 1986. Effect of fertilizer and nematicide treatments on crops grown for biomass. Biomass 11: 243-253.

Muldoon, D.K., and C.J. Pearson. 1979. The hybrid between *Pennisetum americanum* and *Pennisetum purpureum*. Herbage Abstracts 49: 189-199.

Munson, P.J. 1975. Archaeological data on the origins of cultivation in the southwestern Sahara and its implications for West Africa. p.187-210. *In* J.R. Harlan, J.M.J. de Wet, and A.B.L. Stemler (eds.) The origins of African plant domestication. The Hague: Mouton Press.

Nishiyama, I., and N. Kondo. 1942. Chromosome studies in tropical plants I. Seiken Ziho 1: 26-28.

Ozias-Akins, P., E.L. Lubbers, W.W. Hanna, and J.W. McNay. 1993. Transmission of the apomictic mode of reproduction in *Pennisetum*: co-inheritance of the trait and molecular markers. Theor. Appl. Genet. 85: 632-638.

Pandey, J.P., and J.H. Torrie. 1973. Path coefficient analysis of seed yield components in soybeans (*Glycine max* L. Merr.). Crop Sci. 13:505-507.

Pereira, A.V. 1992. Escolha de variedades de capim elefante. p. 47-62. *In* A.M. Peixoto, J.C. de Moura, and V.P. de Faria (eds.) Anais do 10^0 simpósio sobre manejo da pastagem. FEALQ, Piracicaba, Sao Paulo, Brasil.

Powell, J.B., and G.W. Burton. 1966. A suggested commercial method of producing an interspecific hybrid forage in *Pennisetum*. Crop Sci. 6: 378-379.

Rachie, K.O., and J.V. Majmudar. 1980. Pearl millet. The Pennsylvania State Univ. Press. Univ. Park, PA.

Rajasekaran, K., S.C. Schank, and I.K. Vasil. 1986. Characterization of biomass production, cytology, and phenotypes of plants regenerated from embryogenic callus cultures of *Pennisetum americanum* x *P. purpureum* (hybrid triploid napiergrass). Theor. Appl. Genet. 73: 4-10.

Rangaswamy, K. 1935. On the cytology of *Pennisetum typhoideum* Rich. J. Indian Bot. Soc. 14: 125-131.

Rattunde, H.F., Pheru Singh, and J.R. Witcombe. 1989. Feasibility of mass selection in pearl millet. Crop Sci. 29: 1423-1427.

Rau, N.S. 1929. On the chromosome numbers of some cultivated plants of south India. J. Indian Bot. Soc. 8: 126-128.

SAS Institute Inc., 1985. SAS user's guide: statistics. SAS Institute, Inc., Cary, NC.

Sastry, E.V.D., D.S. Narooka, R.K. Sharma, and J.R. Mathur. 1987. Efficiency of S_1 method for population improvement in pearl millet. Current Sci. 56: 778-779.

Schank, S.C. 1986. Interspecific hybridization and clonal selection of *Pennisetum* to increase biomass production. p. 638. *In* W.H. Smith (ed.) Biomass energy development. Plenum Press, New York, NY.

Schank, S.C. 1987. Production of warm season grasses for biomass. p. 305-318. *In* D.L. Klass (ed.) Energy from biomass and wastes x. Elsevier Appl. Sci. Publ., London, and Institute of Gas Tech., Chicago.

Schank, S.C., R.L. Smith, and S.L. Russo. 1989. Characterization of genetic variability among accessions and crosses of napiergrass, *Pennisetum purpureum*. Proc. XVI Intern. Grass. Cong. 1: 341-342.

Schank, S.C., and D.A. Diz. 1991. A seeded type of hybrid hexaploid elephantgrass with a potential for livestock production in the tropics and subtropics. p. A7-A13. *In* Proc. Int. Conf. Livestock in the Tropics, Gainesville, Florida, 5-8 May, 1991. Inst. Food Agric. Sci., Univ. of Florida, Gainesville.

Schank, S.C., and D.P. Chynoweth. 1993. The value of triploid, tetraploid, and hexaploid napier grass derivatives as biomass and (or) forage. Trop. Agric. 70: 83-87.

Schank, S.C., D.P. Chynoweth, C.E. Turick, and P.E. Mendoza. 1993. Napiergrass genotypes and plant parts for biomass energy. Biomass Bioenergy 4: 1-7.

Scheffer, S.M., J.C. de Saibro, and J. Riboldi. 1985. Efeito do nitrogenio, métodos de semeadura e regimes de corte no rendimento e qualidade da forragem e da semente de milheto. Pesq. Agropec. Bras. 20: 309-317.

Silveus, W. 1933. Texas grasses. The Clegg Company. San Antonio, Texas. 782 pp.

Sleper, D.A., C.J. Nelson, and K.H. Asay. 1977. Diallel and path coefficient analysis of tall fescue (*Festuca arundinacea*) regrowth under controlled conditions. Can. J. Genet. Cytol. 19:557-564.

Sollenberger, L.E., G.M. Prine, W.R. Ocumpaugh, W.W. Hanna, C.S. Jones, Jr., S.C. Schank, and R.S. Kalmbacher. 1988. 'Mott' dwarf elephantgrass: a high quality forage for the subtropics and tropics. Florida Agric. Exp. Stn. Circ. S-356. Inst. Food Agric. Sci., Univ. of Florida, Gainesville, FL.

Sollenberger, L.E., G.M. Prine, W.R. Ocumpaugh, W.W. Hanna, C.S. Jones, Jr., S.C. Schank, and R.S. Kalmbacher. 1989. Registration of 'Mott' dwarf elephantgrass. Crop Sci 29: 827-828.

Sollenberger, L.E., and C.S. Jones, Jr. 1989. Beef production from nitrogen-fertilized Mott dwarf elephantgrass and Pensacola bahiagrass pastures. Trop. Grassl. 23: 129-134.

Sollenberger, L.E., C.S. Jones, Jr., K.A. Albrecht, and G.H. Ruitenberg. 1990. Vegetative establishment of dwarf elephantgrass: effect of defoliation prior to planting stems. Agron. J. 82: 274-278.

Spitaleri, R. 1992. Agronomic performance and ensiling characteristics of seeded *Pennisetum* hexaploid hybrids. M.S. thesis. University of Florida, Gainesville.

Sprague, G.F. 1955. Corn and corn improvement. Academic Press, Inc. New York, NY.

Sree Ramulu, K. 1971. Cytomorphology of the progeny of a raw allopolyploid in *Pennisetum*. Cytologia 36: 652-668.

Stapf, O., and C.E. Hubbard. 1934. Pennisetum. p. 954-1070. *In* D. Prain (ed.) Flora of tropical Africa. Vol. 9. Reeve & Co., Ltd; Ashford, England.

Stür, W.W., and L.R. Humphreys. 1987. Seed production in *Brachiaria decumbens* and *Paspalum plicatulum* as influenced by system of residue disposal. Aust. J. Agric. Res. 38: 869-880.

Tcacenco, F.A., and G.N. Lance. 1992. Selection of morphological traits for characterisation of elephant grass accessions. Trop. Grassl. 26: 145-155.

Van Horn, D.L. 1947. Napier x cattail millet cross. Univ. Hawaii Agric. Exp. Sta. Biennial Report, 1946, 25.

Weisner, L.E., and D.F. Grabe. 1972. Effect of temperature pre-conditioning and cultivar on ryegrass (*Lolium* sp.) seed dormancy. Crop Sci. 12: 760-764.

Williams, W.A., M.B. Jones, and M.W. Demment. 1990. A concise table for path analysis statistics. Agron. J. 82: 1022-1024.

Winter, S.R., and E.K. Thompson. 1987. Grazing duration effects on wheat growth and grain yield. Agron. J. 79: 110-114.

Winter, S.R., E.K. Thompson, and J.T. Musick. 1990. Grazing winter wheat: II. Height effects on response to production system. Agron. J. 82: 37-41.

Wofford, D.S., R.V. Frakes, and D.O. Chilcote. 1986. A detached culm technique for seed production of tall fescue in isolation from foreign pollen sources. Crop Sci. 26: 193-195.

Woodard, K.R., G.M. Prine, and W.R. Ocumpaugh. 1985. Techniques in the establishment of elephantgrass (*Pennisetum purpureum* Schum.). Proc. Soil Crop Sci. Soc. Florida. 44: 216-221.

Wright, S. 1921. Correlation and causation. J. Agric. Res. 20: 557-585.

BIOGRAPHICAL SKETCH

Diego Adolfo Diz was born on January 3, 1965, in San Miguel de Tucumán, Argentina. At the youthful age of nine months, he departed from his home country and followed the footsteps of his parents, Adolfo and Martha Diz. As an inquisitive child he roamed around the world, while living in the U.S., Switzerland, and Mexico. At the mature age of 11, he decided to settle back in his home country, Argentina, with the rest of his family. During his high-school years he got involved with 'gauchos' and the lifestyle of the 'Pampas'. He became very attached to the vast expanses of the Argentine Pampas, with its extensive farming and cattle-ranching activities. In 1982 he graduated from high school at the Escuela Escocesa San Andrés. He then attended the Universidad de Buenos Aires from 1983 to 1989, to study 'agronomía'. During these years, he served his military service (1983-84), worked part time as a farm manager (1986-89), worked as a research assistant for the plant physiology department (1986-89, Universidad de Buenos Aires), and obtained a 3 month scholarship to work as a research assistant at the Institut für Pflanzenwissenschaften (ETH), Zurich, Switzerland (1988). He received his Ingeniero Agrónomo degree in 1989. In July of that year, he was married to Daniela Viau, and 3 days later moved to Gainesville, Florida, to begin working towards his Master of Science degree in Agronomy. On October 13, 1991, Daniela and Diego were very fortunate to bring beautiful Malena into their lives. After completing his master's degree in December,

1991, he continued working towards his Ph.D. degree in the same department. His area of specialization is plant breeding, with a minor in food and resource economics.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Stanley C. Schank, Chair
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

David S. Wofford, Cochair
Associate Professor of
Agronomy

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Kenneth H. Quesenberry
Professor of Agronomy

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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